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COVER: The conelike follicetum or fruit aggregate of *Magnolia tripetala* L., an American species of section Rhytidospermum Spach, is the basis for our new cover design. Individual follicles of the fruiting body were used in the devices for other parts of the Journal and for the offprints. The designs were all drawn by Karen S. Velmure, who also planned and prepared the three preceding covers for the Journal, as well as the accompanying devices.

The section Rhytidospermum, of which *Magnolia tripetala* is the type, includes three species of Asia and four to six of America. These are large shrubs or deciduous trees with leaves crowded into false whorls at the end of branchlets, alternate and widely spaced on new shoots. *Magnolia tripetala*, the umbrella-tree or elkwood, is native in rich woods of eastern North America from southern Pennsylvania and West Virginia, south into Florida, and westward through Ohio and Kentucky to Arkansas and Missouri. It is sometimes found escaped from cultivation north into central Massachusetts. In cultivation it has been involved in many hybrid combinations.

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THE ECOLOGY OF AN ELFIN FOREST IN PUERTO RICO, 17. EPIPHYTIC MOSSY VEGETATION OF PICO DEL OESTE [1]

KEITH W. RUSSELL AND H. A. MILLER [2]

THE SUMMIT FOREST of Pico del Oeste has been characterized in detail by Howard (1968). Subsequent authors in this series have contributed specialized treatises which have added significantly to understanding many aspects of an elfin forest. Because elfin forests have sometimes been termed mossy forests, in reference to the mantle of bryophytes borne by even the most diminutive tracheophyte, consideration of mosses and their role in the total vegetation holds special interest. Fulford *et al.* (1970) have correctly indicated that leafy hepatics comprise most of the epiphytic bryoflora. In our study, 23 species of epiphytic mosses have been identified. A comparison of this figure with Fulford's 60 epiphytic Hepaticae suggests that the statement "leafy Hepaticae comprise 90 percent or more of the bryophyte flora" (Fulford *et al.*, 1970) gives too high an estimate. Fulford *et al.* (1971) subsequently compared several sites in the Luquillo Mountains by determining the frequency of liverwort species collected in each of ten localities. Taking a different approach, we have sought to provide a quantitative description of representative epiphytic moss vegetation.

LITERATURE REVIEW

Several investigators have explored the structure and distribution of epiphytic bryophyte communities in temperate regions. Their findings indicate some degree of substratum specificity, definite species associations, consistent patterns of vertical distribution, windward-leeward effects, and manifestations of the microclimate in the growth-form of the epiphytes.

Hale (1952) analyzed the distribution of bryophytes and lichens on ten wind-thrown trees in a virgin forest in north-central Wisconsin. He found

[1] Based in part on a thesis submitted in 1971 by the senior author in partial fulfillment of the requirements for the M.S. degree at the University of Illinois, Champaign-Urbana, Illinois. The field work was assisted by a grant from the National Science Foundation (GB–3975) to Richard A. Howard, principal investigator.

[2] Readers are referred to "Key to the Mosses of Puerto Rico" by H. A. Miller and K. W. Russell in Florida Sci. **38**(3) : 175–182. 1975, which, along with Crum & Steere's Manual (1957), will aid in the identification of Puerto Rican material. *Ed.*

evidence of vertical zonation, host specificity, and community associations. Each epiphyte species had a vertical pattern of distribution reaching a maximum abundance at a characteristic height. Certain cryptogams were found on only single species of trees. Hale suggested that host specificity may be correlated with pH, roughness, and moisture holding capacity of the bark. In a later study, Hale (1965) summarized: "the greatest value in a study of vertical distribution lies in the fact that a broad range of environmental conditions is compressed into the vertical height of a tree, and the development of epiphytic species along this gradient can be accurately measured."

Barkman (1958) considered epiphyte communities on different sides of the same tree. He related differences in such communities to variations in three influential factors: sun exposure, prevailing wind direction, and non-vertical orientation of the trunk. Bark factors, including nutrient supply and acidity, were found to contribute to development or non-development of a lush epiphytic flora. A high-nutrient, neutral bark was rich in epiphytes; low-nutrient, acidic bark had few epiphytes.

Gimingham and Robertson (1950) suggested that growth-form in bryophytes is a reflection of environmental conditions. To test this, they adapted earlier descriptive schemes and categorized twelve growth-forms found in British terrestrial bryophytes. Various bryophyte communities in England were examined, and plants within them were classed as to growth-form. Relative humidity and light intensity were measured for each community. The physical nature of the substratum seemed to influence community structure; the chemical composition of the substratum made little or no difference. Details of community structure could be related to relative humidity and light intensity. From this preliminary work they were able to characterize certain growth-forms as to probable substratum, light intensity, and humidity. A later paper (Gimingham and Birse, 1957) initiated a series of studies on various factors influencing growth-forms in bryophytes. They revised the 1950 classification scheme and stressed that the system presented could be adapted for use in other regions.

Under controlled conditions, Birse (1957) explored the extent to which various growth-forms could be altered by changes in physical factors. She found that the growth-form of some species is more sensitive to changing factors than that of others. "Rough mats," "smooth mats," and some "dendroid" forms developed creeping or slightly ascendant growth with brighter than usual illumination, a moist substratum, and low relative humidity, but "short turfs" and "tall turfs" continued to grow erect. She found that moisture played a larger part in determining these growth-forms than did light intensity.

Iwatsuki (1960) further adapted the Gimingham and Birse growth-form classification and applied it to epiphytic bryophytes in various forest types in Japan. Included were pendulous mosses and other forms present in southern Japan and the tropics, but not represented in Britain. The terms and symbols he employed (now widely used) are as follows: large cushions

(Cu), small cushions (cu), tall turfs (Te), short turfs (t), open turfs (To), tall turfs with creeping main stems (Tc), feather forms (F), dendroid forms (D), rough mats (Mr), smooth mats (Ms), threadlike mats (Mt), thalloid mats (Th), appressed mats (Ap), wefts (W), and pendulous forms (P). Utilizing such traits as growth-form, substratum specificity, and vertical distribution, Iwatsuki recognized, described, and named 33 associations of Japanese epiphytic bryophytes.

Studying epiphyte communities in a mountain beech forest in Japan, Omura *et al.* (1955) and Hosokawa and Kubota (1957) found that relative humidity decreased and light intensity increased from the base to the top of the trees. These workers also discovered three degrees of resistance to desiccation: species most resistant to desiccation inhabited the crown; those least resistant inhabited the base of the trunk; and those intermediate in resistance were intermediate in distribution, primarily inhabiting the trunk. Hosokawa and Odani (1957) correlated daily compensation periods of epiphytic mosses and lichens with vertical distribution. Species which normally grew at stump level attained compensation at about 400 lux, with an optimum intensity of about 10,000 lux. Trunk species attained compensation at about 1200 lux, with optimum intensity values between 10,000 to 20,000 lux. Crown species required 2000 to 6000 lux to reach compensation, while optimum intensity was about 20,000 lux. Hosokawa *et al.* (1964) summarized their work on the relationship between the distribution of corticolous mosses and humidity and light intensity, concluding that "it is then reasonable to suppose that the ecological range of corticolous species is restricted at their lower limits by light and at their upper limits by water."

Biebl (1965) studied humidity and temperature effects on bryophytes from El Yunque Mountain, Puerto Rico, near Pico del Oeste. Working with selected species from the branches of trees and from the forest floor, he noted that those on the forest floor were less resistant to desiccation than those growing on branches. Species from branches showed little effect when subjected to 24 hours of 75% relative humidity, while four of the five species from the forest floor were adversely affected. Both heat and cold resistance of the studied species exceeded measured extremes on Pico del Oeste; therefore, temperature was not considered to be a limiting factor for those species.

Johnson and Kokila (1970) paralleled Biebl's study on resistance to desiccation of some mosses in the West Malaysian tropical rainforest. The species studied comprised two groups relative to their tolerance of four-hour periods of exposure to reduced humidity. Those species which normally occupied exposed sites had high resistance to damage after four hours exposure to 10% relative humidity, while species which normally were not exposed to less than 75% relative humidity were severely damaged. Of special interest was the response of *Leucobryum sanctum* which occupied sites in the Indo-Pacific region ecologically similar to those of *L. martianum* in Puerto Rico. It was little damaged at 44% humidity; at 10% humidity, it was the most sensitive of all mosses studied.

METHODS

Collections for the present study were prepared by William E. McClain, who participated in the Pico del Oeste project during the summer of 1967. With these collections, we sought to determine whether 1) significant substratum specificity existed; 2) vertical zonation could be determined; 3) the vegetation changed from the windward to the leeward side of a single tree; and 4) degree of cover could be incorporated into characterization of epiphytic moss vegetation.

Nine trees, representing five species of angiosperms, yielded 182 community samples (TABLE 1). Collections were annotated as to height above ground, position on the tree (trunk, branch, crown, etc.), and, when pertinent, windward or leeward exposure. Rough field sketches showing the approximate location of each collection were provided for four study trees. Material from each height and each distinct association was collected, with one small tree being dismembered, bagged, and submitted in entirety. Because most collections were bulky or oddly shaped, they were rewetted, divided, dried, and packeted in the laboratory prior to study. Some collections required several packets. On examination of the packets, all moss components were identified according to Crum and Steere (1957) using our key (Miller and Russell, 1975). Each species in a packet was assigned a visual estimate of its percentage composition within that packet. The approximate percentage composition of each species per collection was then calculated. Data in the following tables, as well as all further calculations, were based on these approximations.

Each tree was sketched to assist in visualizing the position of the communities. McClain's sketches, when available, or Howard's (1968) habit sketches were used as guides to tree shape. Collection numbers, species, and percentage composition were noted on the sketches. A reduced sample of one of these, with data, is presented in FIGURE 1. Iwatsuki's (1960) growth-form nomenclature was used.

Of the 182 samples collected by McClain, no mosses were found in 56 samples. Most of the moss-free samples (80%) came from small branches and leaves in the upper portions of the trees. The remaining 126 collections contained 18 moss species representing 14 genera and 10 families. We present the moss data in tabular form to facilitate comparison. The number of collections included in each table depends upon the amount of information provided by McClain: for example, only 23 samples with mosses were annotated as to windward or leeward; heights were indicated or implied on 108 samples.

Presence, degree of cover, and constancy are used frequently in the tables. We have applied these terms as follows:

Presence (P) is the percentage of the examined trees having the indicated moss species present at least one time. For example, the presence value for *Hemiragis aurea* is 89 (TABLE 3), meaning that *H. aurea* was present at least one time on 89% of the trees examined.

TABLE 1. Data on study trees.

TREE NUMBER	TREE SPECIES	HEIGHT (METERS)	DBH (CENTIMETERS)	NUMBER OF SAMPLES	NUMBER OF SAMPLES WITH MOSSES
1	*Eugenia borinquensis*	2.5	5	38	31
2	*Ocotea spathulata*	3.0	5	27	15
3	*Calycogonium squamulosum*	2.2	1.3	17	10
4	*Tabebuia rigida*	4.6	20	36	29
5	*Calyptranthes krugii*	1.9	2.5	12	8
6	*Ocotea spathulata*	1.2	3.8	8	5
7	*Eugenia borinquensis*	2.2	5	15	11
8	*Ocotea spathulata*	1.9	1.3	14	10
9	*Calyptranthes krugii*	2.2	1.3	15	7
	Total			182	126

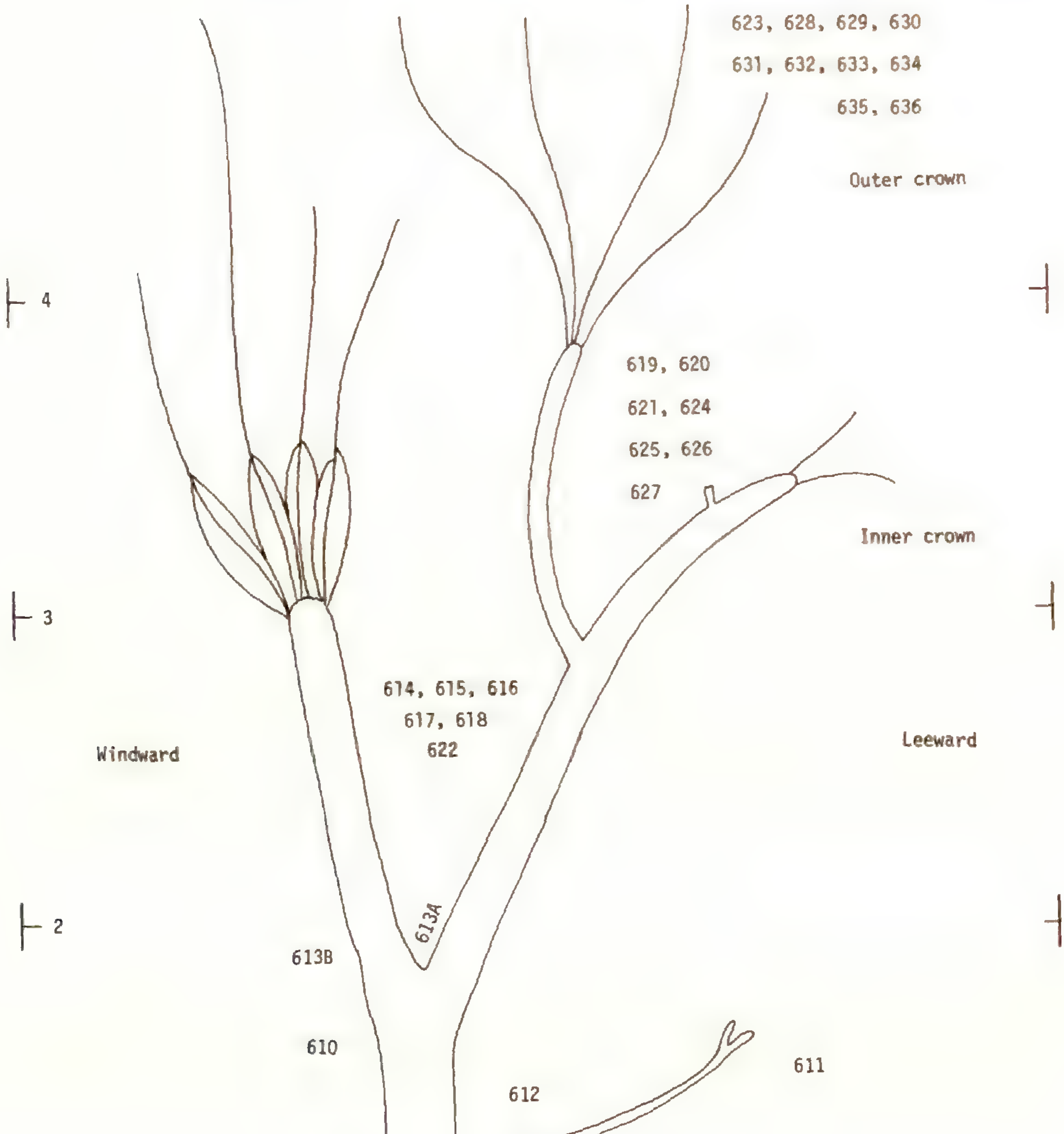

FIGURE 1. Sample mock-up of Tree 4, *Tabebuia rigida*, indicating relative positions of samples collected. Marks indicate one meter height intervals. (Tree outline after McClain's field sketch.)

Degree of cover (D) is the percentage area of cover for the indicated species in each collection averaged for a vertical, or otherwise defined, zone on the tree. Because this is only an approximate value based upon visual judgment, it was indicated as a class according to the following scale:

Class	Cover	Class	Cover
0	trace to 10%	5	51–60%
1	11–20%	6	61–70%
2	21–30%	7	71–80%
3	31–40%	8	81–90%
4	41–50%	9	91–100%

For example, in Table 6 the degree of cover indicated for *Hemiragis aurea* at 0–25% tree height is 1. Thus, *H. aurea* constitutes an average of 11–20% cover in those collections containing *H. aurea* at the tree base. The degree of cover values were calculated as a percentage of all epiphyte cover in the particular category, and were based upon the number of packets of material rather than upon the number of samples. Thus, for example, Tree 6, *Ocotea spathulata*, had five samples with mosses; three contained *Acroporium pungens*, and were considered in figuring the degree of cover for *A. pungens* for this tree. One sample filled four packets with an average of 88% *A. pungens*; another filled two packets with an average of 1%; the last filled 15 packets with an average of 4%. The average was figured as follows:

$$\frac{(4\times 88)+(2\times 1)(15\times 4)}{4+2+15}=19.7,\ \text{class 1.}$$

Constancy (C) is the percentage of collections in a particular class that contained the species in question. For example, the constancy of *Hemiragis aurea* (Table 6) at 0–25% tree height is 50. Thus, *H. aurea* was found in 50% of the moss-containing collections from the lower trunk and base.

DISCUSSION

Of the 18 species of mosses growing as epiphytes in the elfin forest, the families Hookeriaceae and Orthotrichaceae were represented by the most species (five and three, respectively). Both are large and phenotypically diverse families.

Actual height of the study trees varied from 1.2 to 5 meters. Both Howard (1968) and McClain (field notes) indicated that the trees more sheltered from the wind grew taller. Thus, in calculating data for the 1 to 1.6 meter category, canopy epiphytes for the shorter trees and lower trunk species for the 4.6 meter *Tabebuia* were calculated together. Although microclimatic data were lacking, we observed that the community zones were compressed vertically on smaller trees. Accordingly, we also indicate percentage of tree height as well as actual height in Table 2.

From the four best-documented trees in the study, 108 samples had data

TABLE 2. **Distribution of moss species by height on the tree and by percentage of tree height.***

TREE NUMBER	3			1			2			4					
TREE SPECIES	*Calycogonium squamulosum*			*Eugenia borinquensis*			*Ocotea spathulata*			*Tabebuia rigida*			Average	Average	Total
TREE HEIGHT (METERS)	2.2			2.5			3.0			4.6					
	S	D	N	S	D	N	S	D	N	S	D	N	S	D	N
HEIGHT ON TREE (METERS)															
0.3	8	5	2	11	2	7	8	2	5	7	6	3	8.50	3.75	17
0.3–1.0	3	4	1	6	4	6	2	0	2	4	1	4	3.75	2.25	13
1.0–1.7	2	1	5	6	5	9	3	0	2	5	1	3	4.00	1.75	19
1.7–2.2	1	0	2	6	1	3	1	0	1	4	5	4	3.00	1.50	10
2.2–2.8				2	0	2	1	3	6	2	7	3	1.67	3.33	11
2.8										3	6	5	3.00	6.00	5
PERCENTAGE OF TREE HEIGHT															
25	8	5	2	11	2	8	8	2	7	9	3	7	9.00	3.00	24
26–50	3	2	2	6	5	10	3	0	2	6	4	10	4.50	2.75	24
51–75	2	1	4	5	3	4	1	2	3	4	3	6	3.00	2.25	17
76–100	1	0	2	6	2	6	1	6	1	3	6	5	2.75	3.50	14

* The number of species (S), degree of cover (D), and number of collections (N) at each level are indicated.

concerning the height at which collection had been done. The number of moss species and degree of moss cover for these trees are as follows:

PERCENTAGE OF TREE HEIGHT	0–25	26–50	51–75	76–100
Number of samples	34	25	19	30
Number of packets	109	55	47	73
Average percentage of moss cover	40	45	26	37
Number of species	16	8	9	8

Our results indicate that most moss species occurred near the base of the tree, with about half as many appearing at other levels. The degree of cover by mosses in our samples did not show a trend. Mosses were mostly absent from small branches and leaves of the crown, although appressed hepatics were both numerous and diverse in those habitats.

It is clear that researchers doing further field studies of epiphytic bryophyte communities should collect complete, or at least more and larger, samples at each level. This is a particular drawback of data in TABLE 2: some heights were represented by only one or two collections. Because considerable variation occurred from sample to sample, we were cautious in considering whether our samples were representative.

Specificity of certain mosses to particular species of trees was not clearly evident in this study (TABLE 3), although our data did not exclude the possibility. While *Acroporium pungens* and *Macromitrium scoparium* were the only species collected from all trees, *Hemiragis aurea* and *Leucobryum martianum* were collected at least once on every species of tree. *Eugenia* supported the most diverse moss flora, having 14 species on the two specimens examined. *Tabebuia* was next with 12 species. Specimens of *Ocotea* and *Calyptranthes* each had nine moss species. *Calycogonium*, the fifth species, had eight. Except for the 4.6 m. *Tabebuia*, height of the trees seems sufficiently close (TABLE 1) that it would not seem to be a factor affecting diversity.

Comparison of moss distribution with tree families also showed no relationships. *Ocotea* (Lauraceae), *Calycogonium* (Melastomataceae), and *Tabebuia* (Bignoniaceae) were the only representatives of their respective families; Myrtaceae was represented by *Eugenia* and *Calyptranthes*, but a comparison of these two species (four trees) showed no peculiar distribution of epiphytic mosses in our small sample.

Substratum specificity was suggested by *Hookeriopsis acicularis*, which was found only on the specimen of *Calycogonium* and the two specimens of *Eugenia*. The degree of cover and the constancy were similar for *H. acicularis* on each of the three trees.

Definite trends in windward-leeward relationships were not apparent in the samples (TABLE 4) for which McClain indicated wind direction. Only three species changed in degree of cover; three species changed more than 10% in constancy. *Leucoloma serrulatum* appeared to show a clearer relationship to the prevailing wind direction: the degree of cover in this species decreased by two classes, and the constancy by 15%, from the leeward to the windward side. It should be noted that the high values

TABLE 3. Distribution of moss species by tree.*

TREE NUMBER	3		5		9		1		7		2		6		8		4		
	Calycogonium squamulosum		*Calyptranthes krugii*		*Calyptranthes krugii*		*Eugenia boringuensis*		*Eugenia boringuensis*		*Ocotea spathulata*		*Ocotea spathulata*		*Ocotea spathulata*		*Tabebuia rigida*		
	D	C	D	C	D	C	D	C	D	C	D	C	D	C	D	C	D	C	P
Acroporium acestrostegium											0	13							11
Acroporium pungens	1	50	1	88	0	43	2	87	9	73	0	60	1	60	1	70	0	60	100
Callicostella depressa																	0	11	11
Campylopus cygneus			0	25			0	16			0	13	0	20			0	4	56
Hemiragis aurea	6	10	1	25	1	43	0	19			1	27	0	20	1	30	2	14	89
Hookeriopsis acicularis	0	10					0	6	0	9									33
Hookeriopsis obsoletinervis							0	13									0	4	22
Hypnella filiformis							0	6			0	7					0	7	33
Isodrepanium lentulum							0	3											11
Lepyrodontopsis trichophylla	0	10			0	14													22
Leucobryum martianum	1	10	2	25			0	23			0	20	4	20			0	4	67
Leucoloma serrulatum							0	3									1	21	22
Macromitrium perichaetiale					3	14	0	10	3	9							1	25	44
Macromitrium schwaneckeanum									0	18							0	4	22
Macromitrium scoparium	0	100	2	50	0	43	2	30	2	82	1	73	2	100	3	50	3	71	100
Syrrhopodon prolifer	0	20	0	12	2	29	0	58	0	45	0	20							67
Thuidium urceolatum	0	20	0	12							0	7					0	7	44
Vesicularia sp.							0	3											11
Number of species	8		7		6		13		6		9		5		3		12		

* The degree of cover (D), constancy (C), and presence (P) are indicated for each moss species.

TABLE 4. **Distribution of moss species on leeward and windward sides of trees.***

GROWTH-FORM	NUMBER OF COLLECTIONS	LEEWARD (10)		WINDWARD (13)	
		D	C	D	C
Te	*Acroporium pungens*	0	90	1	77
W	*Callicostella depressa*	0	10	0	8
Te	*Campylopus cygneus*	0	10		
W	*Hemiragis aurea*	0	10	0	8
W	*Hookeriopsis acicularis*			0	8
W	*Hookeriopsis obsoletinervis*			0	15
W	*Hypnella filiformis*	0	10	0	8
Cu	*Leucobryum martianum*			0	15
Te	*Leucoloma serrulatum*	2	30	0	15
To	*Macromitrium perichaetiale*	0	10	1	15
To	*Macromitrium schwaneckeanum*	0	10	0	8
To	*Macromitrium scoparium*	0	60	0	46
t	*Syrrhopodon prolifer*	0	20	0	23
W	*Thuidium urceolatum*	0	10		
	Number of species	11			

* Growth-form, degree of cover (D), and constancy (C) are indicated.

for *Leucoloma* (TABLES 4 and 5) are exceptional because of one nearly pure (85%) collection. *Leucoloma* was usually present in small quantities. McClain's systematic collection of 11 samples, taken from various heights on *Tabebuia* and designating prevailing wind direction, is summarized in TABLE 5. Again, *Leucoloma* showed the only substantial change between leeward and windward, but, as noted, the significance of this may be compromised.

McClain's field notes indicate that, with one or two exceptions, the moss species on the forest floor were different from those growing as epiphytes. Studies by Omura *et al.* (1955), Hosokawa and Kubota (1957), Biebl (1965), Johnson and Kokila (1970), Hosokawa and Odani (1957), and Hosokawa *et al.* (1964) have shown that species on or near the forest floor have low resistance to desiccation (and thus require higher humidity), and are able to exist at low light intensities. Those species growing near the tops of trees have adapted to or are tolerant of higher light intensities; in addition, they must be resistant to periods of desiccation. Those in between are exposed to intermediate levels of humidity and light intensity.

Epiphytic mosses of Pico del Oeste fall fairly readily into three groups which seem comparable to the three categories recognized by Hosokawa and collaborators (e.g., 1955, 1957). Data for moss distribution by percentage of tree height are presented in TABLE 6. Characteristic mosses for each of the three vertically stratified epiphyte zones are listed in the following descriptions:

Group I. Species having their greatest occurrence between 0 and 25% of tree height; decreasing or absent above 25%. These species probably

TABLE 5. **Degree of cover of moss species at various heights on leeward (L) and windward (W) sides of Tabebuia rigida.* †**

HEIGHT (METERS)	0–0.3		0.3–0.6		0.6–1.0		1.0–1.4		1.4–1.8	
	L	W	L	W	L	W	L	W	L	W
Acroporium pungens	0	0	1	0	1	0	0	0	2	2
Callicostella depressa	0	0								
Hemiragis aurea	0	0								
Hookeriopsis obsoletinervis				0						
Hypnella filiformis							0			
Leucobryum martianum		0								
Leucoloma serrulatum	8	0	0		0		0			
Macromitrium perichaetiale							0			0
Macromitrium scoparium			0				0	0	0	0
Thuidium urceolatum	0									

* Data are based on eleven collections.
† Cover classes are explained in the text.

TABLE 6. **Vertical distribution of moss species by percentage of tree height.***

	PERCENTAGE OF TREE HEIGHT	0–25		26–50		51–75		76–100	
	NUMBER OF SAMPLES	34		25		19		30	
GROWTH-FORM		D	C	D	C	D	C	D	C
t	*Acroporium acestrostegium*	0	6						
Te	*Acroporium pungens*	0	83	2	88	1	58	0	45
W	*Callicostella depressa*	0	8						
Te	*Campylopus cygneus*	0	22	0	4	0	11		
W	*Hemiragis aurea*	1	50	1	4				
W	*Hookeriopsis acicularis*	0	8					0	3
W	*Hookeriopsis obsoletinervis*	0	11					0	3
W	*Hypnella filiformis*	0	8	0	4	0	5		
F	*Isodrepanium lentulum*					0	5		
W	*Lepyrodontopsis trichophylla*	0	3						
Cu	*Leucobryum martianum*	2	37			0	5	0	3
Te	*Leucoloma serrulatum*	2	14	0	8				
To	*Macromitrium perichaetiale*	0	3	0	15	0	16	6	10
To	*Macromitrium schwaneckeanum*					0	5	0	6
To	*Macromitrium scoparium*	0	39	2	81	2	84	3	74
t	*Syrrhopodon prolifer*	0	28	0	35	0	26	0	16
W	*Thuidium urceolatum*	0	17						
W	*Vesicularia* sp.	0	3						
	Number of species	16		8		9		8	

* Growth-form, degree of cover (D), and constancy (C) are indicated for each species.

require high humidity and survive with low light intensity. (Species marked * in the list do not occur above 0.3 meter.)

**Acroporium acestrostegium* (t); **Callicostella depressa* (W); *Campylopus cygneus* (Te); *Hemiragis aurea* (W); *Hookeriopsis acicularis* (W); *Hookeriopsis obsoletinervis* (W); *Hypnella filiformis* (W); **Lepyrodontopsis trichophylla* (W); *Leucobryum martianum* (Cu); *Leucoloma serrulatum* (Te); **Thuidium urceolatum* (W); *Vesicularia* sp. (W).

Group II. Species most abundant between 26 and 75% of tree height. These species seem to require intermediate levels of humidity and light intensity.

Acroporium pungens (Te); *Isodrepanium lentulum* (F); *Syrrhopodon prolifer* (t).

Group III. Species most abundant above 75% of tree height. These species probably do best at high light intensity and are tolerant of fluctuating humidity.

Macromitrium perichaetiale (To); *Macromitrium schwaneckeanum* (To); *Macromitrium scoparium* (To).

Growth-forms are indicated for species listed above, and in TABLES 4 and 6. Nothing is apparent in TABLE 4 to suggest a relationship between windward-leeward orientation and growth-form. Mosses in Groups I and II are wefts, short turfs, tall turfs, or cushions (only *Leucobryum*). Mosses in Group III are open turfs, but because species of only one genus (*Macromitrium*) were represented, the significance may be somewhat reduced. Our data, in concert with other reports (e.g., Iwatsuki, 1960), indicate that bryophyte growth-forms could be used in a meaningful way by ecologists studying wet tropical vegetation.

The frequency with which one moss species occurred with other species in the same sample, and the constancy of species in all the samples, is summarized in TABLE 7. Reading horizontally for *Campylopus cygneus* to the vertical column for *Hemiragis aurea*, one finds the number 55 at the junction. This means that 55% of the collections containing *Campylopus* also contained *Hemiragis*. *Acroporium pungens* was found in association with over half the species seen; *Syrrhopodon prolifer* occurred together with all except *Callicostella depressa*, and *Macromitrium scoparium* occurred in association with all but three species.

Limited data preclude extensive use of this table, although ecological interrelationships among species, preferences to associate with certain species, and avoidance of others are indicated. It might be expected that certain microclimatic factors inhibit some species and allow others to compete successfully. Perhaps there is inhibition of one species by another. Why, for example, *Hemiragis* did not occur with *Leucoloma* is unknown. *Hemiragis* occurred in 20% of all samples with mosses; *Leucoloma* occurred in 6% of all samples with mosses. Both did best at below 25% of tree height, yet they did not occur together in any of the samples in this study. Further study in the field is required to resolve this and parallel questions.

TABLE 7. **Constancy of species B in collections containing species A.***

		SPECIES B																		
	SPECIES A	*Acroporium acestrostegium*	*Acroporium pungens*	*Callicostella depressa*	*Campylopus cygneus*	*Hemiragis aurea*	*Hookeriopsis acicularis*	*Hookeriopsis obsoletinervis*	*Hypnella filiformis*	*Isodrepanium lentulum*	*Lepyrodontopsis trichophylla*	*Leucobryum martianum*	*Leucoloma serrulatum*	*Macromitrium perichaetiale*	*Macromitrium schwaneckeanum*	*Macromitrium scoparium*	*Syrrhopodon prolifer*	*Thuidium urceolatum*	*Vesicularia* sp.	No. other mosses
2	*Acroporium acestrostegium*		100		50	100			50			100				100	50			
74	*Acroporium pungens*	2		2	13	22	5	3	5	1	1	16	7	10	3	55	33	6	1	14
2	*Callicostella depressa*		67			100			33			33	100							
9	*Campylopus cygneus*	9	100			55	18	9	27			64		18		64	45	18		
20	*Hemiragis aurea*	8	79	12	25		4	4	8			42	12	4		37	37	21	4	
3	*Hookeriopsis acicularis*		100		50	25		25	25		25	75				25	100	25		
4	*Hookeriopsis obsoletinervis*		60		20	20	20		20			40				20	40			
4	*Hypnella filiformis*	20	80	20	60	40	20	20				40	40			60	40	20		
1	*Isodrepanium lentulum*		100														100			
2	*Lepyrodontopsis trichophylla*		50				50					50				50	50	50		50
13	*Leucobryum martianum*	13	93	7	47	67	20	13	13		7		7	7		40	53	13	7	
6	*Leucoloma serrulatum*		86	43		43			29			14				29	14	29		
10	*Macromitrium perichaetiale*		75		17	8						8			8	67	25			17
2	*Macromitrium schwaneckeanum*		100											33		100	67			
69	*Macromitrium scoparium*	2	59		9	11	1	1	4		1	7	2	10	4		17	5		33
26	*Syrrhopodon prolifer*	3	93		16	29	13	6	6	3	3	26	3	10	6	45		6	3	
5	*Thuidium urceolatum*		83		33	83	17		17		17	33	33			67	33			
1	*Vesicularia* sp.		100			100						100					100			

* Constancy of species A in all community samples containing mosses (126) is indicated to the left of species A.

Epiphytic mosses on Pico del Oeste displayed vertical distribution of community associations, though some species occurred in several communities. In general, trunk bases were dominated by *Acroporium pungens*, *Hemiragis aurea*, and *Leucobryum martianum*; canopy dominants were *Macromitrium scoparium* and *Macromitrium perichaetiale*.

This study of mosses is rather broad in scope, and in some respects the findings are inconclusive. Hopefully, it will serve as a starting point for further study to bring knowledge about epiphytic mosses of elfin forests to the same level as that known for epiphytes of some temperate regions. The epilogue provides some additional data on co-inhabiting hepatics of the elfin forest.

EPILOGUE [3]

After regrettably long and personally frustrating delays to completion, the authors have revised and supplemented the original unpublished thesis report and have developed some correlative data pertaining to Hepaticae. Whittier visited Pico del Oeste briefly in January, 1975, mapped the epiphytic flora from a single tree, *Eugenia borinquensis*, in considerable detail, and collected epiphytes on other species as well. The sketch of this tree indicating the collection areas is shown in FIGURE 2. We have included results derived from study of this tree because of the superior characterization of crown populations (especially for leaves) as compared to that aspect of McClain's collections. For this supplement, we have identified the total bryophytic flora, and have estimated cover for hepatic species growing on McClain's Tree no. 4 (*Tabebuia rigida*, FIGURE 1) and for all bryophytes from Whittier's *Eugenia* (FIGURE 2).

The species of mosses found as epiphytes in Pico del Oeste are listed as follows, with indication of those known from *Tabebuia* (T) and *Eugenia* (E): *Acroporium acestrostegium*, *A. pungens* (TE), *Callicostella depressa* (T), *Campylopus cygneus* (TE), *Hemiragis aurea* (TE), *Hookeriopsis acicularis*, *H. obsoletinervis* (T), *Hypnella filiformis* (T), *Isodrepanium lentulum*, *Lepyrodontopsis trichophylla*, *Leucobryum crispum*, *L. martianum* (TE), *Leucoloma serrulatum* (T), *L. schwaneckeanum*, *Leucophanes calymperatum*, *Macromitrium perichaetiale* (T), *M. schwaneckeanum* (T), *M. scoparium* (TE), *Pilotrichum evanescens*, *Syrrhopodon prolifer* (E), *Thuidium urceolatum* (TE), *Trichosteleum sentosum*, *Vesicularia* sp.

Fulford *et al.* (1970, 1971) dealt with the frequency of occurrence in ten study areas in the Luquillo Mountains on the basis of selected collections from a wide variety of substrata. Combining these ten areas, they reported 156 species of leafy liverworts, with 62 species occurring in the elfin forest of Pico del Oeste. Those species which they found and which also occurred on our two study trees are marked F in the following list. Comparison of their lists with ours suggests a great variation in the hepatic flora within the few hectares that comprise the elfin forest study area. It

[3] By H. A. Miller, K. W. Russell, and H. O. Whittier.

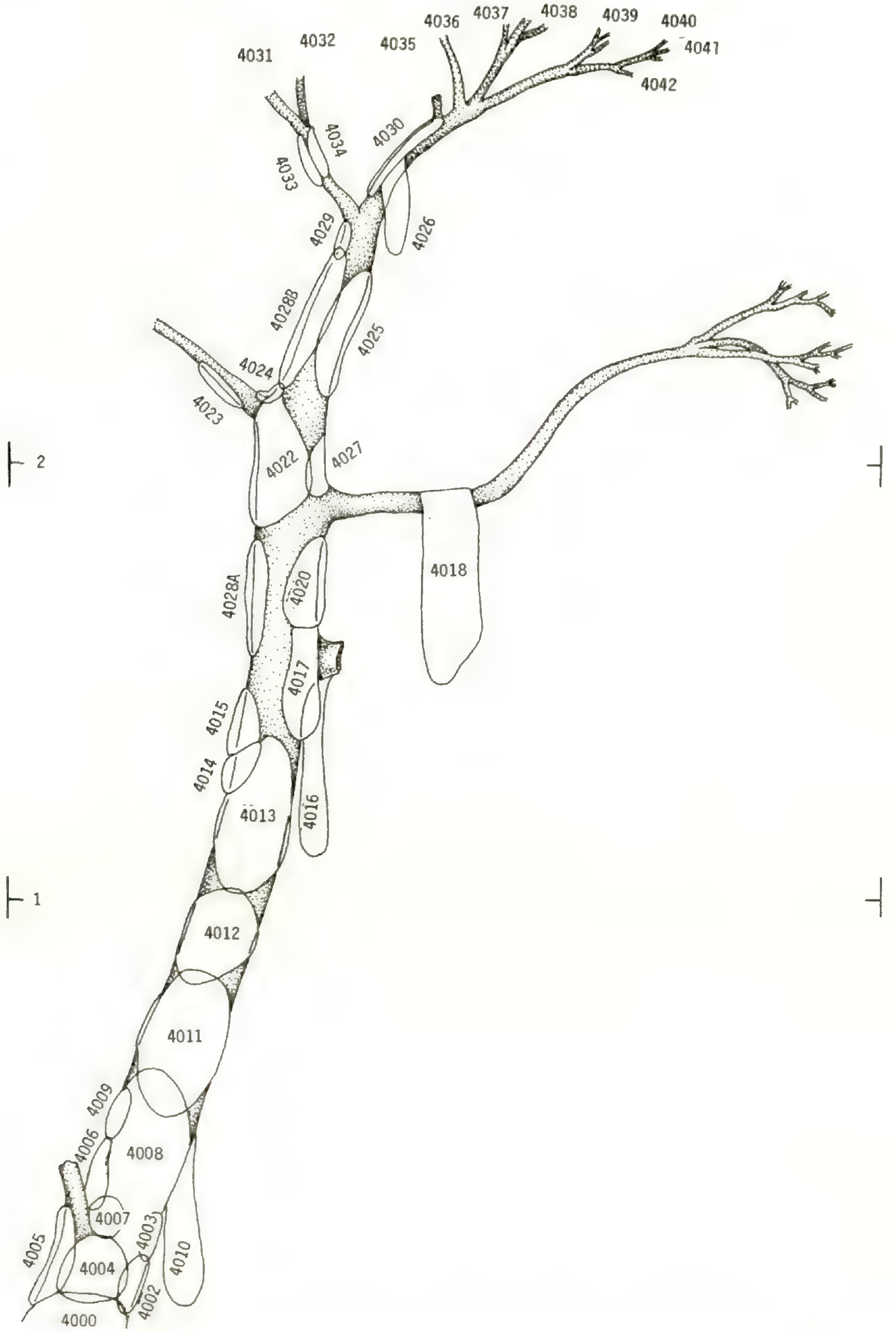

FIGURE 2. Positions and limits of samples collected on *Eugenia borinquensis*. Marks indicate one meter height intervals. (Tree outline after Whittier's field sketch.)

also suggests that with use of broad selective (not random) sampling under field conditions, there is the chance of omission, just as with microscopic examination of a single substratum tree, species present in the total flora can be overlooked due to the narrowness of the sample, chance factors, and subtleties of edaphic and climatic influences.

Epiphytic Hepaticae in the following systematic list were discovered during examination of collections taken by McClain from a specimen of *Tabebuia rigida* (T), and by Whittier from a specimen of *Eugenia borinquensis* (E): *Metzgeria hamata* (TE), *Riccardia fucoides* (E), *R. latifrons* (TE), *R. multifida* (TE), *R. portoricensis* (E), *Herberta divergens* (FTE), *H. pensilis* (FTE), *Bazzania breuteliana* (FE), *B. gracilis* (FTE), *B. hookeri* (FT), *B. longa* (FTE), *B. longistipula* (FE), *B. roraimensis* (FTE), *Lepidozia patens* (FE), *Microlepidozia capillaris* (FE), *Micropterygium carinatum* (FE), *Calypogeia cellulosa* (FE), *C. crenulata* (FE), *Cephalozia caribbeania* (FE), *C.* sp. fragments (E), *Syzygiella rubricaulis* (FT), *Leptoscyphus gibbosus* (FTE), *Plagiochila bidens* (FTE), *P. bursata* (FTE), *P. chinantlana* (FT), *P. jamaicensis* (FE), *P. rutilans* (FT), *P. subbidentata* (FTE), *P. tenuis* (FE), *Radula fendleri* (FTE), *R. inflexa* (FT), *R. saccatiloba* (FTE), *Frullania subtilissima* (FT), *Aphanolejeunea exigua* (TE), *Ceratolejeunea cornuta* (FT), *C. flagelliformis* (FTE), *C. maritima* (FT), *C. patentissima* (FT), *C. valida* (FTE), *Colura clavigera* (FT), *C. rhynchophora* (FTE), *Cyclolejeunea angulistipa* (FE), *Cystolejeunea lineata* (FTE), *Diplasiolejeunea brachyclada* (FTE), *D. pellucida* (FTE), *D. unidentata* (FE), *Drepanolejeunea anoplantha* (FTE), *D. bidens* (T), *D. biocellata* (E), *D. crassiretis* (TE), *D. crucianella* (FE), *D. dissitifolia* (E), *D. evansii* (FE), *D. fragilis* (FTE), *D. inchoata* (TE), *D. lichenicola* (FTE), *D. trigonophylla* (E), *Harpalejeunea heterodonta* (FTE), *H. subacuta* (FT), *H. uncinata* (FTE), *Prionolejeunea aemula* (FTE), *P. aequitexta* (FT), *P. exauriculata* (FT), *P. helleri* (TE), *Rectolejeunea* sp. fragments (E), *Trachylejeunea inflexa* (FTE).

The number of epiphytic hepatic species found on just two trees at Pico del Oeste corresponds closely to the number collected by Fulford *et al.* (1970) on the peak, although the coincidence of species is only about 65%. Their expanded list of Luquillo Mountains hepatics includes over 90% of the species we found, as well as many we did not see on our two trees. One would expect a prolonged and detailed survey of many different kinds of trees to reveal an epiphytic hepatic flora of more than 100 species in the peak forest alone.

The rich admixtures so often encountered in a single collection (APPENDIX) preclude making large pure-stand specimens of sufficient extent for truly satisfactory herbarium reference purposes. Thus, documentation of some species in studies such as ours is necessarily based upon a few stems. The frequency of small individual colonies or minor components is shown in the APPENDIX. FIGURE 2 indicates the extent of individual collections of epiphytic cover. Because of distortions resulting from pressing and drying specimens, estimates of percentages of cover and

orientation may be subject to error, especially for species comprising loose mats or wefts.

Because of difficulties in determining the extent of collections from larger trees, the *Eugenia* selected for this study was stripped as completely as possible of its epiphytic bryophytes. Collections were limited to seemingly natural consociations, which were removed as nearly intact as possible. The boundaries between consociations are indicated roughly by the overlapping regions in FIGURE 2. Despite the time consumed by this type of analysis, we found that future studies would be substantially improved by even more meticulous mapping and specimen removal, with windward and leeward aspects figured separately.

Review of the vertical distribution of bryophytes on single trees of *Tabebuia* and *Eugenia*, summarized in FIGURES 1 and 2 and the APPENDIX, reveals relationships between height on the tree and community composition. Differences become apparent. For example, some moss and hepatic taxa were largely restricted to tree bases below one meter and did not appear on branches or leaves. Others occurred most often on middle and upper trunks, in contrast to species seemingly limited to ultimate branches and/or leaves. Leafy hepatics were the almost exclusive inhabitants of the outer tree crown.

Differences suggested by the data in the APPENDIX may or may not be valid. Differences in sampling methodology may make the distinctions somewhat questionable in the sense that absence of a species on *Tabebuia* might be due to sampling oversight. *Campylopus cygneus* was restricted to near the base of the *Eugenia*, but occurred only once in collections from *Tabebuia* (in a specimen taken between two and three meters above the ground). Whether this was a result of random or chance variation, or was due to an oversight in collecting, is unclear; in this instance it seems likely that some edaphic or microclimatic factor was responsible. *Leucoloma serrulatum* was a common species below one meter on *Tabebuia*, but no *Leucoloma* was found among collections from *Eugenia*. The real meaning of the information will become clear only with further tree analyses.

Mosses such as *Campylopus*, *Leucobryum*, and *Leucoloma* were characteristic trunk base inhabitants, sometimes representing as much as 80% of the "cover" or species composition of samples taken in the first meter above the ground. Hepatics such as *Riccardia*, *Calypogeia*, *Cephalozia*, and *Plagiochila* were common on lower trunks in the same associations with the mosses; *Plagiochila*, however, seemed less limited, with certain species of this genus extending into the second and third meter level above the ground.

Middle trunk species were characterized by species of *Macromitrium*, which seldom occurred below the second meter level, but which sometimes extend into the crown. *Acroporium pungens* was a representative eurivalent moss, common near the trunk base, occurring in fair abundance (to 5%) in samples three to four meters above the ground on *Tabebuia*, and present at least in a single sample four to five meters above the ground.

Among the hepatics, *Herberta, Bazzania, Cystolejeunea,* and (to a lesser degree of constancy) *Plagiochila* exhibited similarly euryvalent distribution from ground level to the four to five meter level, suggesting much broader tolerances in microclimatic response.

Upper branches did not appear to support stenovalent mosses; only broad-ranging taxa such as *Macromitrium* and *Acroporium* appeared commonly on both trees. As already noted, the upper branches were characteristically the domain of hepatics, with *Radula, Leptoscyphus, Diplasiolejeunea, Drepanolejeunea, Rectolejeunea, Trachylejeunea, Frullania, Ceratolejeunea,* and others almost exclusively restricted to this area. Curiously, while some species of *Riccardia* (e.g., *Riccardia fucoides*) appeared restricted to the first meter above the ground near the bases of the trunks, others (e.g., *Riccardia multifida*) seemed to exclude this region of the trunks, selecting higher or upper portions.

Epiphyllous forms included only Hepaticae on the two study trees, although mosses may occasionally appear as epiphylls in the elfin forest. Typical epiphyllous taxa were *Colura clavigera, C. rhynchophora,* and *Ceratolejeunea patentissima.* Four out of six collections of *Colura rhynchophora* from *Eugenia* were as epiphylls; *C. clavigera* occurred only once as an epiphyll on *Tabebuia. Drepanolejeunea* appeared as an epiphyll as well as on smaller branches of both *Tabebuia* and *Eugenia.* Two species of *Harpalejeunea* were found as epiphylls on *Eugenia,* but they occurred only on the bark of *Tabebuia.* Fourteen species of epiphyllous hepatics appeared on *Eugenia*; the fact that only five were reported from *Tabebuia* suggests substratum influence. Such a conclusion must be accepted cautiously, however, since it may be due to differences in sampling methodologies. We found that older leaves of *Eugenia* supported a richer bryoflora than the two species listed by Howard (1969). Because discrimination in the field is difficult, future samples which must be studied remote from the collecting site should represent substantial and comparably prepared harvests from selected representative trees.

Assembly of data correlating microclimatic parameters with vertical stratification and cryptogamic community composition could become important in creating ecological models by which microclimatic factors could be determined from presence or absence of key species or communities. Potential applications might be made, for example, in tropical forestry, where conditions for optimal seedling development could be determined with considerable precision from field observations applied to the model. However, with the limited cryptogamic community data now available, the best models would probably be inadequate or premature.

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APPENDIX. Vertical distribution and percentage cover of bryophytes on two trees from the elfin forest on Pico del Oeste.*

Tabebuia rigida (McClain's Tree 4)

0–1 m. MUSCI: *Leucoloma serrulatum*, 603–6, 604–5, 605–85, 607–2, 608; *Leucobryum martianum*, 604; *Macromitrium scoparium*, 607; *Callicostella depressa*, 603–7, 604–2, 605–2; *Hemiragis aurea*, 603–40, 604–5, 605; *Hookeriopsis obsoletinervis*, 606–3; *Hypnella filiformis*, 603–2; *Thuidium urceolatum*, 603, 605; *Acroporium pungens*, 604–2, 605, 606–8, 607–16, 608–12, 609–5. HEPATICAE: *Metzgeria hamata*, 603, 604, 605–3; *M.* sp., 609; *Riccardia latifrons*, 607, 608–5, 609; *Herberta divergens*, 604, 606, 607, 608; *H. pensilis*, 609; *Bazzania gracilis*, 605, 606; *B. longa*, 605, 607, 609; *B.* sp., 604, 606; *Plagiochila bidens*, 606, 607; *P. bursata*, 603–3, 604–3, 605–3, 606, 609–30; *P. chinantlana*, 603, 605; *P. subbidentata*, 606, 607–30, 608–50, 609; *Radula fendleri*, 605, 609; *R. inflexa*, 603; *R. saccatiloba*, 606; *Harpalejeunea subacuta*, 606; *Prionolejeunea aemula*, 603; *Cystolejeunea lineata*, 603, 605, 607, 608; *C. exauriculata*, 606; *C. helleri*, 605, 606; *Trachylejeunea inflexa*, 607.

1–2 m. MUSCI: *Leucoloma serrulatum*, 610; *Macromitrium perichaetiale*, 612–2, 613B–2; *M. scoparium*, 610–4, 611–4, 612–6, 613A–5, 613B–5; *Hypnella filiformis*, 610; *Acroporium pungens*, 610–5, 611–6, 612–7, 613A–23, 613B–28. HEPATICAE: *Metzgeria hamata*, 610; *Riccardia latifrons*, 610–5; *Herberta divergens*, 610, 611–95, 612–20, 613–95; *H. pensilis*, 610–5; *Bazzania longa*, 610–5, 612–20, 613–2; *Plagiochila bursata*, 610; *P. chinantlana*, 610, 613; *P. subbidentata*, 610–10, 612–25, 613; *Radula fendleri*, 610; *Ceratolejeunea valida*, 612; *Cyclolejeunea angulistipa*, 613; *Cystolejeunea lineata*, 610–2, 611, 612, 613.

2–3 m. MUSCI: *Campylopus cygneus*, 614; *Macromitrium perichaetiale*, 614; *M. scoparium*, 614–31, 615–97, 616–89, 618–12; *Acroporium pungens*, 614–18, 615, 616. HEPATICAE: *Metzgeria hamata*, 614, 617, 618; *Riccardia latifrons*, 614, 617, 618; *Herberta divergens*, 614, 615–75, 616–5, 617, 618, 622–40; *H. pensilis*, 614–2; *Bazzania gracilis*, 617; *B. longa*, 614, 617, 622; *Plagiochila chinantlana*, 614; *P. jamaicensis*, 614, 617; *P. subbidentata*, 614, 618; *Ceratolejeunea valida*, 614, 617; *Cyclolejeunea angulistipa*, 614, 622; *Cystolejeunea lineata*, 614, 615, 616, 617; *Trachylejeunea inflexa*, 617–2, 622.

3–4 m. MUSCI: *Macromitrium perichaetiale*, 619–2, 620–2; *M. schwaneckeanum*, 620; *M. scoparium*, 619–25, 620–5, 621–44, 622–79, 624–5, 625–81, 626–100; *Acroporium pungens*, 619, 620–2, 622, 625–5. HEPATICAE: *Metzgeria hamata*, 619; *Riccardia latifrons*, 619; *Herberta divergens*, 619–50, 620–90, 621–20, 624, 625, 627; *Bazzania gracilis*, 620, 621, 625; *B. hookeri*, 624, 626; *B. longa*, 620, 627; *Plagiochila bidens*, 625; *P. chinantlana*, 625, 627; *Radula saccatiloba*, 624, 626; *Frullania subtilissima*, 627; *Aphanolejeunea exigua*, 627; *Ceratolejeunea valida*, 624, 627; *Cyclolejeunea angulistipa*, 626; *Cystolejeunea*

* The height on the tree where a collection originated is given first, followed by the species name and collection numbers. Estimated percentage of cover for the species within a single collection follows the dash after the collection number; if the cover is one per cent or less no dash is used. Epiphyllous collections are so identified regardless of their height above the ground. Each tree is treated separately.

lineata, 620, 624, 625; *Drepanolejeunea inchoata*, 627; *Harpalejeunea subacuta*, 619; *Trachylejeunea inflexa*, 619–5, 620–2, 621–2, 625, 627.

4–5 m. MUSCI: *Macromitrium perichaetiale*, 623–100, 635–65; *M. scoparium*, 632–100, 633–35, 636; *Acroporium pungens*, 635. HEPATICAE: *Riccardia multifida*, 628, 630, 631, 633, 634; *Herberta divergens*, 632, 633, 635; *Bazzania longa*, 628, 631, 632, 633, 635, 636; *B. roraimensis*, 635; *Syzygiella rubricaulis*, 636; *Leptoscyphus gibbosus*, 633; *Plagiochila bidens*, 628, 630, 631, 633, 636; *Radula fendleri*, 636; *R. saccatiloba*, 630, 631, 633; *Frullania subtilissima*, 628, 630, 631, 633, 634, 635, 636; *Ceratolejeunea cornuta*, 634; *C. flagelliformis*, 633; *C. patentissima*, 628, 630, 631, 633, 634, 635, 636; *C. valida*, 628, 630–70, 631, 633–50, 634, 635, 636; *Colura rhynchophora*, 635; *Cystolejeunea lineata*, 628, 635, 636; *Diplasiolejeunea brachyclada*, 633; *Drepanolejeunea anoplantha*, 628, 633; *D. bidens*, 634; *D. crassiretis*, 628, 636; *D. fragilis*, 628, 633, 636; *D. inchoata*, 628, 633, 634, 635, 636; *D. lichenicola*, 635, 636; *Harpalejeunea heterodonta*, 633; *H. uncinata*, 623; *Prionolejeunea aemula*, 630; *P. aequitexta*, 630, 633; *Trachylejeunea inflexa*, 623, 630, 634.

Epiphylls. HEPATICAE: *Ceratolejeunea patentissima*, 629; *Colura clavigera*, 629; *C. rhynchophora*, 629; *Diplasiolejeunea pellucida*, 629; *Drepanolejeunea fragilis*, 629; *D. inchoata*, 629.

Eugenia borinquensis (Whittier's Tree)

0–1 m. MUSCI: *Campylopus cygneus*, 4003, 4005–3, 4007, 4008, 4009–10, 4010–10; *Leucobryum crispum*, 4010–10; *L. martianum*, 4000, 4002, 4003–10, 4004–80, 4005–75, 4006–3, 4007–80, 4008–80, 4009–30, 4011–80; *Syrrhopodon prolifer*, 4002, 4003, 4004–5, 4006, 4007, 4008, 4010; *Hemiragis aurea*, 4010–30; *Thuidium urceolatum*, 4009, 4010; *Acroporium pungens*, 4000, 4002, 4003, 4005–3, 4006, 4007. HEPATICAE: *Riccardia fucoides*, 4000–80, 4002–20, 4003–10, 4004–15, 4005, 4006, 4009–15, 4010; *R. portoricensis*, 4004, 4005, 4007, 4008–2, 4012, 4013; *Herberta divergens*, 4002; *H. pensilis*, 4009–5; *Bazzania gracilis*, 4010–20; *B. longa*, 4008; *B. roraimensis*, 4006; *Lepidozia patens*, 4002–2, 4004, 4005, 4006, 4007; *Microlepidozia capillaris*, 4009–7, 4010; *Micropterygium carinatum*, 4012–30; *Calypogeia cellulosa*, 4004, 4005, 4010, 4012; *Cephalozia caribbeania*, 4002–3, 4003–10, 4004–3, 4005, 4006, 4007, 4008–15, 4010–5, 4012; *Plagiochila bidens*, 4004, 4005, 4012; *P. bursata*, 4004–3, 4011–2; *P. chinantlana*, 4002, 4004, 4005, 4007, 4011–4, 4012–10; *P. subbidentata*, 4002–8, 4004–11, 4005–11, 4006–8, 4007–12, 4009, 4011–4, 4012–9; *Aphanolejeunea exigua*, 4003; *Ceratolejeunea maritima*, 4007; *Colura rhynchophora*, 4007; *Cystolejeunea lineata*, 4000, 4004–4, 4006, 4007, 4008, 4011–2, 4012–5; *Prionolejeunea aemula*, 4009; *P. helleri*, 4003.

1–2 m. MUSCI: *Leucobryum martianum*, 4016, 4028B; *Macromitrium scoparium*, 4022; *Hemiragis aurea*, 4022; *Acroporium pungens*, 4013–3, 4014, 4015, 4016, 4028B–2. HEPATICAE: *Riccardia fucoides*, 4015–20; *R. latifrons*, 4022, 4027; *R. portoricensis*, 4016; *Herberta divergens*, 4022–5, 4027–10; *H. pensilis*, 4014, 4015–5, 4016–20; *Bazzania breuteliana*, 4013; *B. gracilis*, 4016; *B. longa*, 4014–2, 4015–5, 4016, 4017–10, 4018–90, 4020–95, 4022–50, 4028B–10, 4027–25; *B. longistipula*, 4013–70, 4018; *B. roraimensis*, 4018, 4027; *Lepidozia patens*, 4014, 4028B–10; *Microlepidozia capillaris*, 4020–3, 4027–7; *Micropterygium carinatum*, 4014, 4016, 4028B; *Calypogeia cellulosa*, 4015, 4016, 4017, 4027; *C. crenulata*, 4014, 4018; *Cephalozia caribbeania*, 4015, 4028B–3; *Plagiochila bidens*, 4014; *P. bursata*, 4014–6, 4016, 4017–50, 4018; *P. jamaicensis*,

4013; *P. chinantlana*, 4013–10, 4014, 4015–20, 4016–5, 4017–2, 4018, 4020, 4028B–3; *P. rutilans*, 4022; *P. subbidentata*, 4015–7, 4022–7; *Ceratolejeunea valida*, 4016; *Cystolejeunea lineata*, 4013, 4014–2, 4015–20, 4016–10, 4017–20, 4018, 4020–3, 4022–10, 4027–5, 4028B–20; *Drepanolejeunea anoplantha*, 4016.

2–3 m. MUSCI: *Syrrhopodon prolifer*, 4030; *Macromitrium scoparium*, 4025, 4030, 4031–25; *Acroporium pungens*, 4023–50. HEPATICAE: *Metzgeria hamata*, 4024–5, 4025–5, 4038; *Riccardia latifrons*, 4024–60, 4025–10, 4026–20, 4028A, 4033–35; *R. multifida*, 4028A, 4042; *R. portoricensis*, 4024, 4028A; *Herberta pensilis*, 4023, 4030; *Bazzania breuteliana*, 4023, 4030; *B. gracilis*, 4030; *B. longa*, 4023, 4024, 4025–20, 4028A, 4029–85, 4030, 4033; *B. longistipula*, 4026–15, 4028A, 4030; *B. roraimensis*, 4023, 4028A, 4030; *Lepidozia patens*, 4024–2, 4025; *Microlepidozia capillaris*, 4024–6; *Calypogeia cellulosa*, 4025, 4026–2, 4030; *C. crenulata*, 4023; *Cephalozia caribbeania*, 4023; *Leptoscyphus gibbosus*, 4042; *Plagiochila bidens*, 4026, 4031, 4032, 4033, 4036, 4037, 4040, 4041, 4042; *P. bursata*, 4042; *P. jamaicensis*, 4025, 4028B, 4030; *P. chinantlana*, 4023, 4025–10, 4026–15, 4028A, 4029, 4030, 4032, 4033, 4037, 4042; *P. subbidentata*, 4023–7, 4025–9, 4026–5, 4028A–11, 4030–14, 4032–9, 4033–7, 4036–40, 4042; *Radula fendleri*, 4033; *R. saccatiloba*, 4031, 4034–25; *Aphanolejeunea exigua*, 4042; *Ceratolejeunea flagelliformis*, 4039, 4042; *C. valida*, 4028A, 4030, 4032, 4036, 4038, 4039–50, 4040, 4041, 4042; *Colura rhynchophora*, 4032, 4036, 4037, 4038, 4039, 4041, 4042; *Cyclolejeunea angulistipa*, 4029; *Cystolejeunea lineata*, 4023, 4025, 4030; *Diplasiolejeunea pellucida*, 4042; *D. unidentata*, 4037, 4039; *Drepanolejeunea anoplantha*, 4028A, 4032, 4033–2, 4036; *D. biocellata*, 4041; *D. crassiretis*, 4023, 4031, 4040, 4042; *D. crucianella*, 4039, 4042; *D. dissitifolia*, 4037, 4038, 4041; *D. evansii*, 4036, 4037, 4038, 4039, 4040; *D. fragilis*, 4037–20, 4038, 4039, 4041; *D. inchoata*, 4036, 4037, 4038, 4039, 4042; *D. lichenicola*, 4039, 4040, 4041, 4042; *Harpalejeunea heterodonta*, 4032, 4042; *H. uncinata*, 4036, 4037, 4038, 4042; *Prionolejeunea aemula*, 4028A, 4029, 4030, 4032, 4033, 4034–10; *P. helleri*, 4032; *Trachylejeunea inflexa*, 4023; *Rectolejeunea* sp., 4032, 4042.

Epiphylls. HEPATICAE: *Ceratolejeunea flagelliformis*, 4039; *C. valida*, 4038, 4040; *Colura rhynchophora*, 4037, 4039, 4041, 4042, 4038; *Cyclolejeunea angulistipa*, 4029 on *Plagiochila; Drepanolejeunea crucianella*, 4039, 4042; *D. dissitifolia*, 4037, 4041; *D. evansii*, 4038, 4039, 4040; *D. fragilis*, 4039, 4041; *D. inchoata*, 4037, 4038, 4039; *D. lichenicola*, 4039, 4042; *Harpalejeunea heterodonta*, 4037; *H. uncinata*, 4038; *Prionolejeunea aemula*, 4029 on *Plagiochila*.

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THE MARTYNIACEAE IN THE SOUTHEASTERN UNITED STATES[1]

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MARTYNIACEAE Stapf in Engler & Prantl,
Nat. Pflanzenfam. IV. 3b: 265. 1895.

(UNICORN-PLANT FAMILY)

Strong-scented annual herbs [or perennials, sometimes with tuberous roots], pubescent with both glandular and nonglandular hairs. Leaves exstipulate, simple, long-petioled, opposite to alternate, entire to sinuate [dentate or lobed], cordate at base, sometimes inequilaterally so. Inflorescence racemose, terminal. Flowers perfect, zygomorphic, hypogynous, pediceled, each axillary to a bract. Calyx of 5 sepals, zygomorphic, bibracteolate at base, either synsepalous and spathaceous, more or less unequally 5-lobed, split abaxially to base [or of free sepals]. Corolla sympetalous, the tube cylindrical at base, this cylindrical portion about equaling [or much longer than] the calyx, the throat campanulate [or infundibular], the limb 5-lobed, somewhat 2-lipped, aestivation imbricate, the upper lobes external. Androecium of 4 [2] didynamous, fertile, alternate stamens and usually 1 [3] staminode, all inserted on the corolla near junction of tube and throat, included in throat; anthers dorsifixed, becoming more or less connate, with placentoids, 4-sporangiate, biocular at maturity, locules dehiscing longitudinally and introrsely; pollen

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The length of the paper and the number of references are quite out of proportion to the representation of Martyniaceae in our flora, especially considering that *Proboscidea louisianica* cannot with certainty even be called a native of the area. I hope that the greater than usual biological interest of the family and the bringing together of much of a widely scattered literature will justify the extra pages.

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spheroidal, reticulate, apparently nonaperturate. Gynoecium syncarpous, carpels 2; stigma 2-lipped, the lips thin, broad and flat, sensitive to touch; style elongate, included in or slightly exserted from the throat; ovary unilocular, with 2 parietal intruded placentae, each placenta expanded into a broad lamella, T-shaped in cross-section; ovules many [few], unitegmic, tenuinucellar, anatropous; embryo sac development normal (Polygonum type); endosperm *ab initio* cellular, with haustoria. Fruit a 2-valved drupe, imperfectly 5- [4-] locular, terminated by an upcurved beak developed from proximal portion of the style and longer [or shorter] than the fruit body; exocarp thick, fleshy, deciduous in 2 valves; endocarp woody, sculptured [or echinate], crested along the adaxial [and sometimes abaxial] suture, dehiscing along both sutures [sometimes only distally, then more or less indehiscent proximally], the beak splitting into two elongate [or short], sharp-pointed "horns"; seeds numerous [few], relatively large, rugose-tuberculate; endosperm thin, membranaceous; embryo straight, oily, with fleshy, epigeal cotyledons. TYPE GENUS: *Martynia* L.

The Martyniaceae comprise about 20 species. Van Eseltine, the most recent monographer of the family, recognized five genera; his treatment has since been followed by most workers, although a few (e.g., Chittenden) include, in an enlarged (and more than a century old) concept of *Martynia*, the genera *Ibicella* (Stapf) Van Eseltine, *Proboscidea* Schmidel, and *Martynia* L. sensu stricto (= *M. annua* L.). Two genera (one native and one introduced) occur in the conterminous United States. One species of *Proboscidea* represents the family in the southeastern United States.[2] The family is indigenous to tropical and warm temperate areas of the New World from southern (southwestern?) United States to Uruguay and northern Argentina; a few species have been introduced as weeds into the Old World.

As with many "Personatae," the taxonomic status of the Martyniaceae is debatable. The family has been included in Bignoniaceae (Jussieu, Kunth), Gesneriaceae (Baillon), and Pedaliaceae (Bentham & Hooker, Decaisne, Hutchinson [1926], and, more recently, Backer, Heine, and Humbert). A close relationship between Martyniaceae and Gesneriaceae has been re-emphasized, mainly on anatomical grounds, by Cortesi. The Martyniaceae now are most commonly considered to be a separate family, the New World counterpart of the Pedaliaceae, from which they differ in their unilocular ovary and parietal placentae.

A characteristic vegetative feature of Martyniaceae is their glandular

[2] *Ibicella*, a South American genus of three species, has been collected as a waif in the southeastern United States, e.g., on "ballast" in Alabama (Van Eseltine). I find, however, no evidence that the genus has become established in our area, although it is naturalized in parts of California. It can be distinguished from *Proboscidea* as follows:

Calyx synsepalous and spathaceous, 5-lobed, split to the base abaxially; fertile stamens 4; endocarp body sculptured. ..... *Proboscidea.*
Calyx of 5 free sepals; fertile stamens 2; endocarp body echinate. ..... *Ibicella.*

hairs, which consist of a one- to several-celled uniseriate stalk and a several-celled head. The copious, sticky secretion of the hairs gives the plants a distinctive aminoid odor and clammy feel. That many small insects are trapped by the secretion on the leaves and stems has been noted by various authors and can be seen on both living plants and herbarium specimens. The function of the hairs and their secretion is unknown. Insectivory immediately comes to mind, and this indeed has been strongly affirmed for *Martynia* [i.e., *Ibicella*] *lutea* by Mameli, who reported a proteolytic enzyme in the secretion and stated unequivocally that the plant "è una pianta insettivora." Earlier, Fermi & Buscaglioni got negative results in a search for such an enzyme in *Martynia*. Manganaro suggested that the secretion of *Ibicella lutea* "se trate de un aparato capturado de la humedad atmoférico, dado que la planta . . . es seguramente xerófila."

The fruits of Martyniaceae are certainly the family's outstanding characteristic. As these fruits mature, the endocarp becomes woody, the exocarp fleshy. An upwardly-curved beak (longer than the fruit body in our genus and in *Ibicella*, shorter than it in *Craniolaria* and *Martynia*) develops from the proximal portion of the style, and it is the long beak of some Martyniaceae that evidently suggested the name "unicorn plant." At fruit maturity, in an unsurpassed example of vegetable ecdysis, the exocarp sloughs off in two valves, splitting along the abaxial and adaxial sutures. Concurrently, the endocarp, crested along one or both sutures and sculptured, echinate, or ribbed, begins to dehisce distally along the sutures. The beak splits into two sharp-pointed, hooked, and (in ours) elongate horns.

The fruits are adapted for dispersal through attachment to mammals by means of the hooked horns: the literature records sheep, mules, horses, cattle, bison, and panthers (!) as vectors but surely there are others. Aided by the stylar horns, the fruits cling to fetlock, tail, mane, or body fur. In our genus, seeds presumably drop out as the fruits are carried about. In *Martynia*, the seeds seem to be freed only by crushing or rotting of the endocarp.

Nomenclature for the fruit type of the Martyniaceae is problematical. The fruit has been called, *inter alia*, a "capsule with fleshy deciduous exocarp and woody endocarp," a "woody many-seeded capsule," a "capsule with deciduous pericarp" (!), a "ligneous drupe," a "drupaceous capsule," a "subdrupaceous capsule," a "drupaceous follicle," and a "pod." Authors unwilling to commit themselves use simply "fruit." I have seen only one paper on fruit classification that mentions Martyniaceae: Gusuleac included *Martynia* among "Steinfrüchten" in his category "Eusynkarpe Früchte." I call the fruit of Martyniaceae a drupe even if the choice does not fit into the classical definition of a drupe, which emphasizes a fleshy or pulpy, indehiscent exocarp (the exocarp plus mesocarp of some authors), a hard or bony, indehiscent endocarp, and a single carpel and seed. Fruits of *Prunus* best exemplify this concept. In practice, however, the term "drupe" is used for many fruits not fitting this definition.

Characteristics making martyniaceous fruits aberrant as drupes can be seen in other drupaceous fruits, although, so far as I am aware, not all in the same one. The fleshy exocarp of the Martyniaceae separates in two valves to reveal the endocarp or "stone" (Nafday calls it a "pyrene"), and a similarly dehiscent exocarp is found in the almond (*Prunus amygdalus*) and in *Bursera Simaruba* (three valves). The endocarp of Martyniaceae dehisces along two sutures (at this point in its development the endocarp is a remarkable mimic of a "typical" capsule); dehiscent endocarps seem to be rare among drupes but can be seen occasionally in *Prunus*. The drupes of Martyniaceae are bicarpellate, and those of *Rhamnus, Melia, Ilex, Empetrum, Elaeis*, and certain other genera also consist of more than one carpel. The "stones" of Martyniaceae contain many or as few as four seeds, or even sometimes two in *Martynia* (Nafday); "stones" with more than one seed occur also in other drupes, e.g., *Borassus* (three), *Orbigyna* (three to eight), *Melia* (six), and even *Prunus* (sometimes two). There appears, then, to be no way to avoid calling the fruits of Martyniaceae drupes, although they are unlike that fruit type as generally typified by *Prunus*. Such a situation emphasizes the need, as far as classification and nomenclature of fruits are concerned, of a thorough review and revision.

Gametic and somatic chromosome numbers (mostly undocumented) reported for Martyniaceae indicate diploid numbers of $2n = 30$ (Martini, Perry) or $2n = 32$ (Covas & Schnack) for *Ibicella* (*Proboscidea*) *lutea*; $2n = 32$ for *Martynia annua* (Srinivasan); and $2n = 30$ for *Proboscidea fragrans* (Perry, Sugiura) and *P. louisianica* (Gaiser, Martini, Perry, Snow).

Several Martyniaceae are grown in gardens for their showy flowers and curious fruits. A few are widely distributed weeds that, in some regions, are considered noxious. Some species are used in folk medicine, and some produce edible roots, young fruits, and seeds.

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1. **Proboscidea** Schmidel, Icones Plantarum (Keller ed.) 49. *tab. 12, 13.* 1763.

Erect to decumbent, glandular-pubescent, strong-scented annual herbs [or tuberous-rooted perennials]. Leaves simple, long petioled, opposite to alternate, entire to sinuate [or palmately or pinnately lobed], cordate and sometimes inequilateral at base. Racemes usually exceeding leaves, few- to many-flowered, the axis lengthening in fruit, as do the pedicels. Calyx

FIGURE 1. **Proboscidea.** *P. louisianica*: a, branch with flower and young fruit, × ¼; b, lateral view of flower to show calyx, bractlets, and expanded stigma, × 1; c, flower with stigmatic lobes nearly closed together after stimulation, × 1; d, flower in partial longitudinal section to show position of style and stamens, × 1½; e, flower with calyx and most of corolla removed to show stamens and style from below, × 2; f, cross section of ovary oriented as in flower to show parietal placentation, × 8; g, ovary in vertical section, cut between the two placentae, showing one placenta and its ovules, × 8; h, mature

bibracteolate at base, synsepalous, spathaceous, more or less unequally 5-lobed, split to base on abaxial side, eventually deciduous. Corolla tube cylindrical at base, this cylindrical portion about equalling calyx, the throat campanulate [or infundibular], the limb somewhat 2-lipped, 5-lobed, the lobes rounded. Androecium of 4 fertile stamens and one short staminode, included in throat, the abaxial pair of fertile stamens the longer; anthers of each pair becoming connate side by side, and the proximal tips of anthers of the longer stamens becoming connate to distal tips of anthers of the shorter. Gynoecium somewhat exceeding [or about as long as] stamens; style about three times as long as ovary; stigma lips sensitive, obovate [obovate-oblanceolate], included in or slightly exserted from the throat. Drupe with thick, dehiscent exocarp, terminated by an upcurved beak 1½–3 [1¼–3½] times as long as the body; endocarp woody, sculptured, crested adaxially [sometimes also abaxially], dehiscent along both sutures, the beak splitting into two elongate, sharp-pointed "horns"; seeds several to many, black [rarely white], rugose-tuberculate; endosperm thin, delicate, papery, whitish. TYPE SPECIES: *P. louisianica* (Miller) Thellung. (*Martynia louisianica* Miller). (Name from Greek, *proboskis*, in allusion to the long-beaked fruit.) — UNICORN PLANT.

A genus of 14 species (9 recognized by Van Eseltine, 5 described since) native from the southern (southwestern?) United States south to Peru. Our species, *P. louisianica* (*Martynia Proboscidea* Gloxin), $2n = 30$, is widespread in the southern United States, but whether it is indigenous to the south*eastern* United States is uncertain. Occurring in meadows, fallow fields, waste places, and garbage dumps, along roadsides, and as a garden weed, it has spread to the Old World where in some areas (e.g., Australia) it is considered noxious.

The flowers are protandrous and, according to published accounts, pollinated by bees. The insects seek nectar produced by glandular hairs on the filament bases and on the area of the corolla tube between these bases; they may also take pollen. The pollination mechanism of *P. louisianica* is noteworthy (Thieret). The sensitive stigma is distal to the connate anthers along the median line of the upper surface of the corolla tube; its two lips, with their receptive inner surfaces, close together rapidly after even the slightest touch. An insect ascending the tube first contacts the stigma; pollen on its back is "scooped" off by the lower lip, which then closes against the upper lip, trapping the pollen between them and preventing its dislodging as the insect leaves the flower. Next, the insect rubs against the connate introrse anthers and is re-dusted with pollen. As the insect exits, the closed stigma lips may prevent or significantly reduce transfer of pollen of a flower to the stigma of that flower, simply because the receptive surfaces of the stigma are not exposed.

In a series of touches, the time required for closing of the stigma lips

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fruit, the fleshy exocarp dehiscing and beginning to fall away from endocarp, × ½; i, endocarp after drying, × ½; j, seed with tough seed coat, × 4; k, embryo, oriented as in seed, × 4.

increases hardly at all, but the time for their spreading apart again increases considerably (from 5 minutes after the first touch to 25 minutes after the eighth) — the phenomenon of "stigmatic fatigue."

After sloughing off of the exocarp, the beak of the fruit of *P. louisianica* splits into two sharp-pointed, hooked, elongate horns that, with further drying, become oriented in a way reminiscent of the tusks of a mammoth, with their tips pointing toward each other or even overlapping. After dropping from the plant, the endocarps usually lie with their horns pointing upward, the position in which they are most likely to hook onto animals and thus be dispersed. The common names "mule-grab" and "cow-catcher" for *P. louisianica* attest to the effectiveness of this adaptation for dispersal.

In sheep-raising areas (e.g., Arizona, Australia), the endocarps, with their long, hooked horns, get tangled in the wool of sheep (as do those of *Ibicella lutea*) and interfere with shearing. The horns have been known to work into eye sockets of grazing animals, and stock are recorded as having starved to death when a *Proboscidea* or *Ibicella* endocarp has clamped their jaws together (Gardner). Froggatt reported that "men employed in cutting [*Martynia* (*Ibicella*) *lutea* for weed control] become extremely dizzy in the head after working on it for any length of time." It would be interesting to know the physiological basis of this and whether the same reaction would occur with *P. louisianica*.

Young fruits of *P. louisianica* (and probably other species of *Proboscidea*) can be made into pickles (Harrington) and have even been grown commercially for this purpose (Van Eseltine). They pose no gastronomic threat, however, to *Cucumis sativus*. The dried dehisced endocarps are made into "floral" decorations. Cultivation of *P. louisianica* for its oil-rich seeds (60% fat in the embryo) has been suggested (Bailey & Long, 1915a, 1915b). Strips split from mature *Proboscidea* endocarps are woven, as dark designs, into baskets by certain southwestern Amerindians; Hevly (1970a) mentions "semicultivated strains" of *P. parviflora* being so used. *Proboscidea louisianica* is an attractive, easily grown garden ornamental. Its fetid aroma and its tendency to become somewhat weedy are its main drawbacks. Its seeds germinate slowly and irregularly, but if Heit's method of removing the outer, dark coat and the delicate, whitish endosperm layer before the seeds are planted is followed, germination will usually occur within 10 days.

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NEW SPECIES AND A NEW COMBINATION FROM THE BAHAMAS, CAICOS AND TURKS ISLANDS

DONOVAN S. CORRELL

EXTENSIVE FIELD EXPLORATIONS during the past several years have enabled me to study at first hand the flora of the Bahamas, Caicos and Turks islands. Among the numerous collections obtained during these explorations are more than 100 species that are new to the flora of the islands; species that have their origin mainly in the Greater Antilles.

With further intensive study of many of my collections, the species described here were discovered. Holotypes have been placed in the herbarium of the Arnold Arboretum, Harvard University; isotypes are in the Fairchild Tropical Garden Herbarium, and elsewhere when available.

RANUNCULACEAE

Clematis orbiculata Correll, sp. nov. FIGURE 1.

Suffrutex scandens ad plus minusve 5 m. altus. Folia 3- vel raro 5-foliolata, 3–9 cm. longa; foliola herbacea, orbiculares, apice apiculata, 1.5–3.5 cm. diametro, raro lobulata. Achenium brunneum, 3–3.5 mm. longum, cauda plumosa 5–6 cm. longa, pilis argenteis ad 3 mm. longis.

TYPE. Bahamas, Great Exuma, vine on shrubs in coppice about Forrest, January 10, 1975, *D. S. Correll 44074* (A, holotype).

Woody climber to 5 m. or more high; stems and branches glabrous, ribbed. Leaves opposite, glabrous, 3–9 cm. long, 3- or rarely 5-foliolate; petiole 1.5–3.5 cm. long. Leaflets herbaceous, orbicular, apiculate at the broadly rounded apex, 1.5–3.5 cm. in diameter, rarely lobate; petiolule 3–10 mm. long. Peduncles terminal or lateral on leafy branches. Flowers not seen. Achene brown, obliquely elliptic, compressed, 3–3.5 mm. long, 2–2.5 mm. wide, slightly hirsute; achene tail 5–6 cm. long, plumose with silvery hairs to 3 mm. long.

The orbicular leaflets readily separate this plant from *Clematis bahamica* (O. Kuntze) Britton and the closely allied, if not conspecific, *C. dioica* L., that are characterized by having ovate to elliptic and acute to acuminate leaflets with subcordate to obtuse bases. *Clematis orbiculata* has also been collected in pinelands, Eight Mile Rocks, Grand Bahama, during February 5–13, 1905 (*Britton & Millspaugh 2393* (NY)).

EUPHORBIACEAE

Euphorbia hieroglyphica Correll, sp. nov. FIGURE 2.

Frutex erectus ad 6 dm. altus, caule simplici 8 mm. crasso, superne ramosus dichotome. Rami ramulique laeves. Stipulae minutae, triangulari-

ovatae, rigidae, paginis interioribus albo-ciliolatis. Folia laevia, oblique suborbiculata vel elliptica, basi et apice rotundata, 5–12 mm. longa, 4–8 mm. lata, pagina inferne pallida, pagina supra viridis intricate conspicueque reticulata, petiolis gracilibus 1–2 mm. longis. Involucrum solitarium, turbinatum, purpureum. Glandes cupreae.

TYPE. Bahamas, Crooked Island, in open coppice along road to Turtle Sound, west of Church Grove; flowers (glands) dark red; leaves thin, February 17, 1975, *D. S. Correll 44346* (A, holotype; FTG, isotype).

Shrub erect, to 6 dm. tall, with a simple woody stem 8 mm. thick, dichotomously open-branched above. Main branches and branchlets smooth. Stipules minute, triangular-ovate, rigid, white-ciliolate on inner surface. Leaves opposite, with slender petioles 1–2 mm. long, smooth, obliquely suborbicular to elliptic, rounded at base and apex, 5–12 mm. long, 4–8 mm. wide, pale on lower surface, intricately and conspicuously veined on green upper surface. Involucre solitary, turbinate, purplish-red, about 3 mm. long including the short stipe. Glands reddish-brown. Capsule (immature) glabrous.

This species differs from the allied *Euphorbia lecheoides* Millspaugh and its close relatives, *E. wilsonii* Millspaugh and *E. exumensis* Millspaugh, in being more shrubby and in having smooth, not papillose, leaves and young stems. Also, its thin, herbaceous leaves have a clear and distinctive venation pattern on their upper surface, and are inequilaterally rounded rather than fleshy-thickened and more or less cordate at the base.

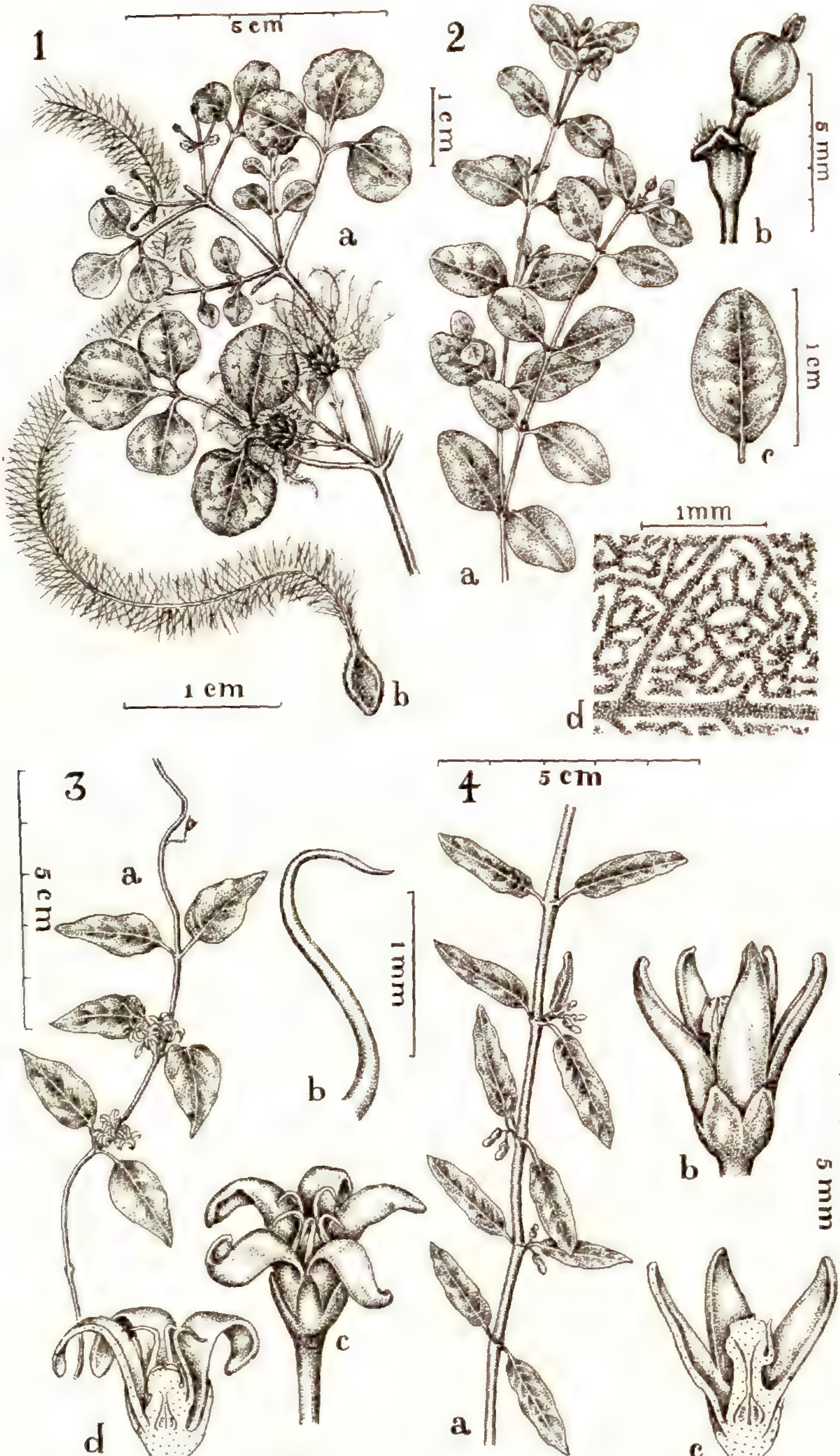
MYRTACEAE

Psidium androsianum (Urban) Correll, comb. nov.

Eugenia androsiana Urban in Fedde, Rep. Sp. Nov. **13:** 467. 1915. (Type: Bahamas. Andros, Mangrove Cay, coppice, near Lisbon Creek, shrub 1 m. tall; stems diffused, January 16–19, 1910, *J. K. Small & J. J. Carter 8496* (F, NY)).

Urban founded his *Eugenia androsiana* on sterile plants. Based on my field observations, I would say that his narrow-leaved plants grew in dense shade. I have collected plants in the same coppice community that have narrow leaves similar to those in the type material as well as leaves that are about twice as wide. In other words, the leaves range from linear-elliptic to narrowly oblong-elliptic. The vernicose, non-veiny upper surface of the leathery leaf contrasts markedly with the veiny upper surface of the thick, herbaceous leaf of *Psidium longipes* (Berg) McVaugh.

Britton and Millspaugh accepted Urban's species in their *The Bahama Flora,* where they keyed it out on the basis of its small linear leaves. They stated under the species, "When flowers of this shrub are obtained, they may show it to belong to one of the other genera of Myrtaceae." On April 22, 1969, John Popenoe obtained flowering material of this plant from Deep Creek, South Andros (FTG). Popenoe's collection establishes the true generic identity of this species.



FIGURES 1–4. *Clematis orbiculata*: 1a, section of vine; 1b, achene. *Euphorbia hieroglyphica*: 2a, branch of plant; 2b, hypanthium with immature fruit; 2c, leaf; 2d, enlarged section of upper surface of leaf. *Cynanchum sigmoideum*: 3a, section of vine; 3b, crown segment; 3c, flower, natural position; 3d,

ADDITIONAL COLLECTIONS SEEN. All are sterile and all are from Andros. Long Bay Cays, August 18–September 10, 1906, *L. J. K. Brace 5007* (F); Long Bay Cays Section, coppice, Crow Hill, shrub; branches irregular, January 25–27, 1910, *J. K. Small & J. J. Carter 8694* (F, GH, US); in coppice just south of Andros Town, shrub about 2 m. tall, January 31, 1974, *D. S. Correll & R. K. Godfrey 41399* (FTG); sterile shrubs 0.3–1.5 m. tall, in dense forest about 1.2 miles west of Congo Town airstrip, September 25, 1974, *D. S. Correll 43549, 43550* (FTG); about 1 mile west of Congo Town and airport, burned over pineland, hammock adjacent to airstrip and pines, sterile at this season, July 9, 1975, *W. T. Gillis 12505* (A).

ASCLEPIADACEAE

Cynanchum sigmoideum Correll, sp. nov. FIGURE 3.

Suffrutex intricate volubilis, tenuis, glaber. Folia ovata vel ovato-elliptica, 1–3 cm. longa, 5–15 mm. lata. Cymae paucifloriferae. Corolla 2–3.5 mm. longa. Coronae laciniae graciles, filiformes, typice sigmoideae vel aliquantum contortae, gynostegio sessili 2–3-plo longiores.

TYPE. Bahamas, North Bimini, vine on various shrubs and other plants in open coppice on north edge of Alice Town; flowers cream-white; corona longer than gynostegium, January 16, 1975, *D. S. Correll 44170* (A, holotype; FTG, isotype).

A slender, intricately twining, glabrous vine. Leaves ovate to ovate-elliptic, 1–3 cm. long, 5–15 mm. wide. Cymes few-flowered. Calyx lobes triangular-ovate, acute, with scarious margins, somewhat pubescent just below the base. Corolla 2–3.5 mm. long, the lobes linear-lanceolate, acute, papillose on the inner surface. Crown segments slender-filiform, typically sigmoid or somewhat contorted, 2 to 3 times as long as the sessile gynostegium.

Britton and Millspaugh, in their 1920 *The Bahama Flora*, erroneously included this plant in the Cuban *Metastelma hamatum* Grisebach (= *Cynanchum caribaeum* Alain). That species has much shorter, rather broad crown segments that are, at most, merely recurved over the gynostegium.

Cynanchum sigmoideum is centered in the Biminis, with outlying stations on New Providence.

ADDITIONAL COLLECTIONS EXAMINED. Biminis, North Cat Cay, April 15, 1904, *C. F. Millspaugh 2333* (F, NY); Cat Cay, flowers white, May 11, 1905, *L. J. K. Brace 3747* (F, NY); North Bimini, vine on shrubs on edge of coppice on white-lands, Easter Key, flowers creamy-white, April 17, 1974, *D. S. Correll 42106* (FTG); North Bimini, vine trailing over shrubs in open beach coppice in vicinity

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longitudinal section through flower. *Cynanchum stipitatum*: 4a, section of vine; 4b, flower, in natural position; 4c, longitudinal section through flower. *Drawn by Priscilla Fawcett.*

of East Wells, flowers greenish-yellow, corona longer than gynostegium, January 17, 1975, *D. S. Correll 44179* (FTG, NY). New Providence, November 11, 1879, *L. J. K. Brace 514* (NY); Lyford Cay isthmus, over bushes near beach, flowers pale yellowish, March 4, 1946, *Otto Degener 19059* (NY).

Cynanchum stipitatum Correll, sp. nov. FIGURE 4.

Suffrutex volubilis, glaber; caulis infernus erecto-ascendens, sparsim supra dichotome ramosus. Rami graciles salignique, apice volubiles. Folia anguste elliptica vel elliptico-lanceolata, acuta vel longi-acuminata 2–4 cm. longa, circa 1 cm. lata. Flores pauci. Sepala triangulari-ovata, circa 1.2 mm. longa, aliquantum basi imbricata, in facie dorsali papillosa. Corollae lobi elliptico-lanceolati, 2.5 mm. longi, pagina interiore subglabra. Gynostegium stipite gracile 1 mm. longo.

TYPE. North Caicos, in cut-over area along Bottle Creek airstrip; vine trailing on ground and over shrubs, September 3, 1974, *D. S. Correll 43436* (A, holotype).

Sprawling, glabrous, viny shrub, often tinged or marked with purplish-red; stem erect-ascending, the lower portion 5 mm. or more thick, sparsely dichotomously branched above. Branches slender and willowy, twining at their apices. Leaves opposite or sometimes 1 to several at a node, narrowly elliptic to elliptic-lanceolate, acute to long-acuminate, 2–4 cm. long, to about 1 cm. wide. Few-flowered. Sepals triangular-ovate, obtuse, about 1.2 mm. long, somewhat overlapping at base, dorsally papillose, with a purplish-red demarcation within the ciliolate scarious margins. Corolla lobes elliptic-lanceolate, internally subglabrous, 2.5 mm. long. Gynostegium with a slender stipe 1 mm. long.

This species is allied to the more northern *Cynanchum northropiae* (Schlechter) Alain in having a slender stipe that supports the gynostegium. The plant differs from that species, however, in its somewhat frutescent habit. The long, simple main stem that produces slender, dichotomous branches, the typically narrowly elliptic-lanceolate, acuminate leaves, differently adorned sepals and internally subglabrous corolla lobes are distinctive.

RUBIACEAE

Borreria felis-insulae Correll, sp. nov. FIGURE 7.

Herba porrecta vel applanata ad 3 dm. lata. Rami primarii numerosi, basi valde lignea, ramos secundarios congestos aspectu decumbentem producentes. Folia linearia, acuto-cuspidata, glabra, dorsalia carinata, 5–8 mm. longa, circa 1 mm. lata, plerumque nodos multo excedentia, ad caulem adpressa vel aliquantum recurvo-patula. Inflorescentia pluriflora ad apices ramorum. Calyx circa 3 mm. longus, duobus lobis linearibus acutisque. Corolla infundibuliformis, caesia, 2–2.5 mm. longa, lobis reflexis.

TYPE. Bahamas, Cat Island, in sandy, open soil on edge of coastal coppice, Hawk's Nest; plant forming flat, spreading mats; flowers lavender-tinged, November 25, 1975, *D. S. Correll 46301* (A, holotype; FTG, isotype).

Plant forming flat, spreading mats to 3 dm. across. Primary branches numerous from a strong woody base, giving rise to many congested, secondary branches that create an upswept appearance. Stipules triangular-ovate, about 1 mm. long. Leaves linear, acute-cuspidate, glabrous, dorsally keeled, 5–8 mm. long, about 1 mm. wide, mostly much exceeding the nodes, appressed to the stem or somewhat recurved-spreading. Inflorescences at apices of branches, several-flowered. Calyx about 3 mm. long, the 2 lobes linear and acute. Corolla funnelform, lavender-tinged, 2–2.5 mm. long, the lobes reflexed. Fruit immature.

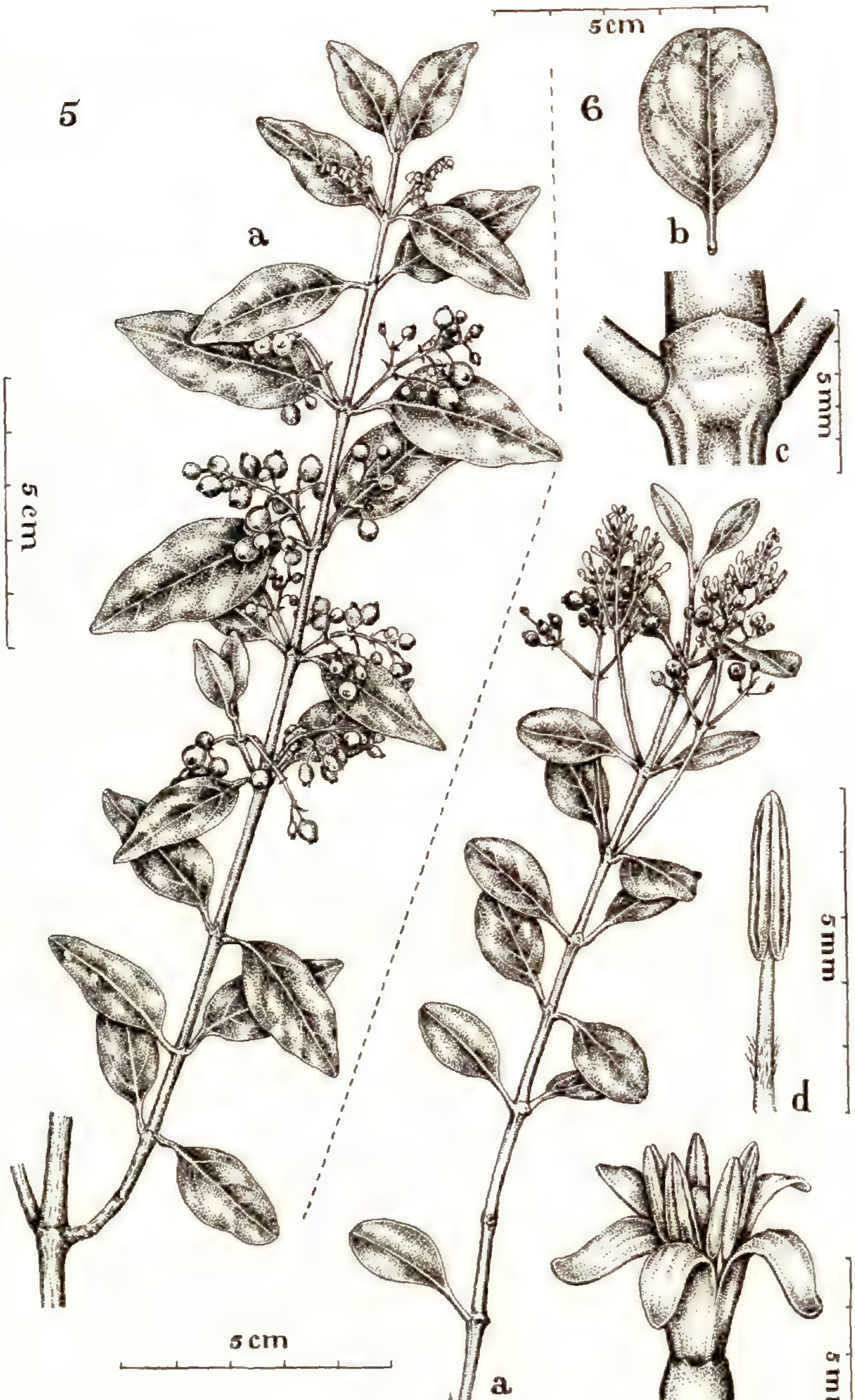
The southern Bahamian, Caicos and Turks perennial plants of *Borreria* that revolve about *B. thymifolia* Grisebach intrigued N. L. Britton during the preparation of his and C. F. Millspaugh's *The Bahama Flora* (1920) to the extent that he described what he considered to be five species unique to our flora. In my opinion, these complex plants remain not only intriguing, but also a most difficult problem; they are not to be taken too lightly.

Some of the plants appear to represent species that have long been isolated on a particular island or group of islands. For instance, on Grand Turk I could find no species other than *B. thymifolia* (No. *46556*), described from that island in 1864. Again, the only plants that I could find on Little Inagua (No. *45993*) were identical to type material of *B. inaguensis* Britton, which was collected on that island in 1904. Also, the only plants that I could find on South Caicos (No. *43444*) were referable to *B. saxicola* Britton (= *B. brittonii* Standley), the type of which was collected there in 1911. This apparent uniqueness, of course, does not hold for all of the species, such as *B. bahamensis* Britton (*B. wilsonii* Britton), described from a collection made on Crooked Island in 1906, and *B. savannarum* Britton, described from a collection made on Great Inagua in 1904. I have not only collected material duplicative of these types on the above islands (Nos. *44425* and *41653*, respectively), but I have also collected specimens of these plants on other islands.

In line with the above, the only collection that I have seen from Cat Island, other than what I have collected, is a specimen obtained by Britton and Millspaugh (No. *5824*) northwest of The Bight during March 1–6, 1907. The original label was marked only "Borreria," but marked lightly on the sheet in pencil is "cf. B. bahamensis Britt.," to which it does not belong. The plant is identical to those I collected 68 years later and represents a new taxon for this genus.

Chiococca stricta Correll, sp. nov. FIGURE 5.

Frutex columnaris, usque ad 2 m. altus, habitu rigide erecto, denso. Rami stricti vel valde ascendentes. Folia crassa, superne nitida, ovato-



FIGURES 5, 6. *Chiococca stricta*: 5a, fruiting branch in natural position. *Erithalis diffusa*: 6a, flowering and fruiting branch, note roots; 6b, typical shape of leaves; 6c, section of stem to show stipule; 6d, stamen; 6e, flower, in natural position. *Drawn by Priscilla Fawcett.*

elliptica vel elliptico-lanceolata, apice obtusa, basi late cuneata, 3–4 cm. longa, 1.5–2.5 cm. lata. Panicula quam folium subtentum brevia.

TYPE. Bahamas, Cat Island, along trail on coppice-covered hills just north of New Bight; plant with rigidly erect growth habit, thickly foliaged, to about 2 m. tall, November 23, 1975, *D. S. Correll 46265* (A, holotype; FTG, isotype).

Shrub columnar, with a rigidly erect, dense growth habit, to about 2 m. tall. Branches strict or strongly ascending. Stipules connate, forming an aristate sheath. Leaves thick, glossy above, ovate-elliptic to elliptic-lanceolate, obtuse at apex, broadly cuneate at base, 3–4 cm. long, 1.5–2.5 cm. wide; petiole about 4 mm. long. Panicle shorter than the subtending leaf. Pedicel slender, 3–4 mm. long. Corolla not seen. Calyx puberulent on inner surface, the minute lobes triangular and ciliolate. Fruits white, compressed, about 5 mm. long.

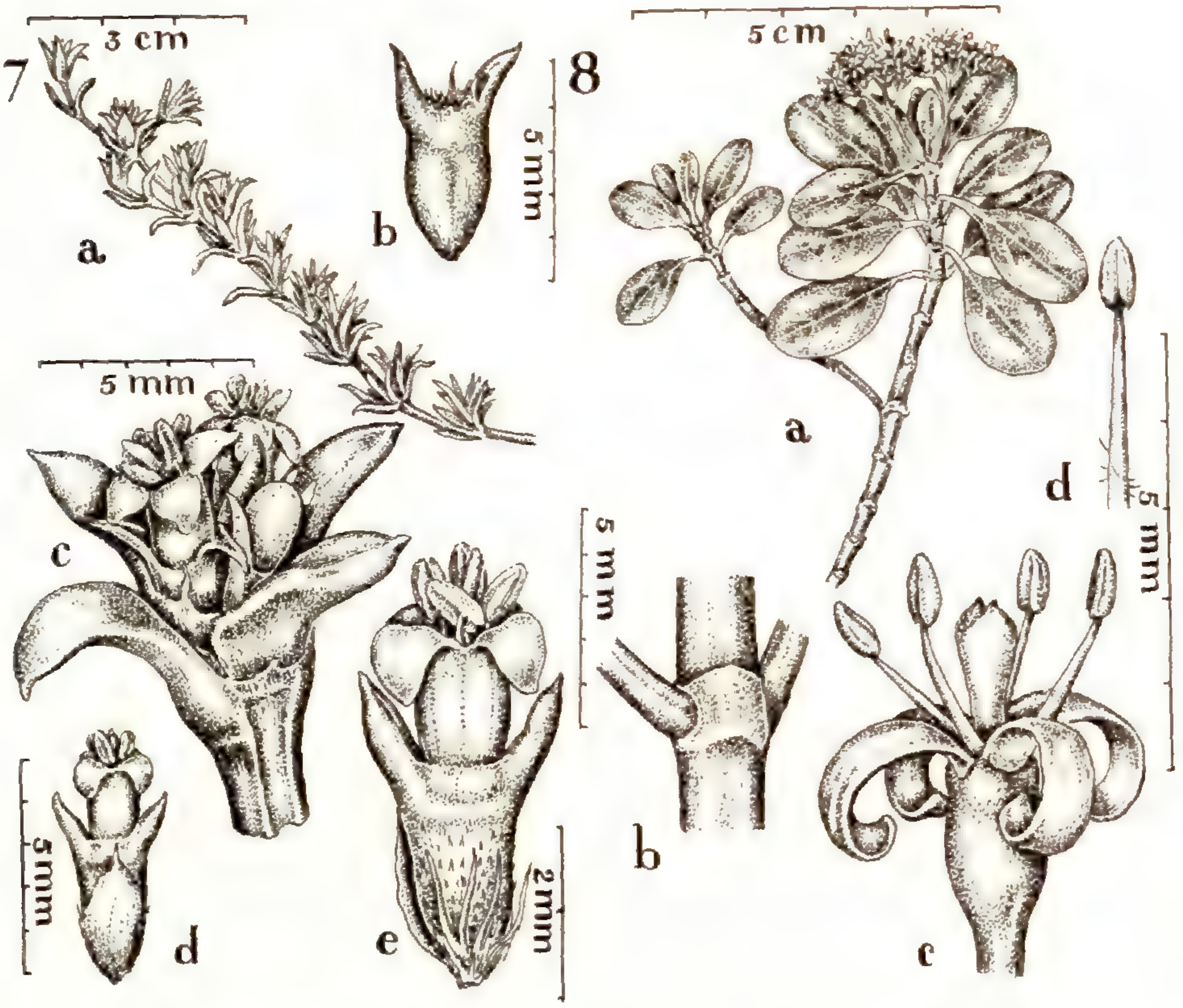
This plant contrasts markedly with our other two viny species of *Chiococca, C. alba* (L.) A. S. Hitchcock and *C. parvifolia* Wullschlagel (*C. pinetorum* Britton). It is most nearly related to the latter species. The plant forms a dense columnar mass 2 m. or more in height. It is rigidly erect, with its relatively short branches strict or strongly ascending instead of being spread at right angles to the main stem, as is the case with our other two species.

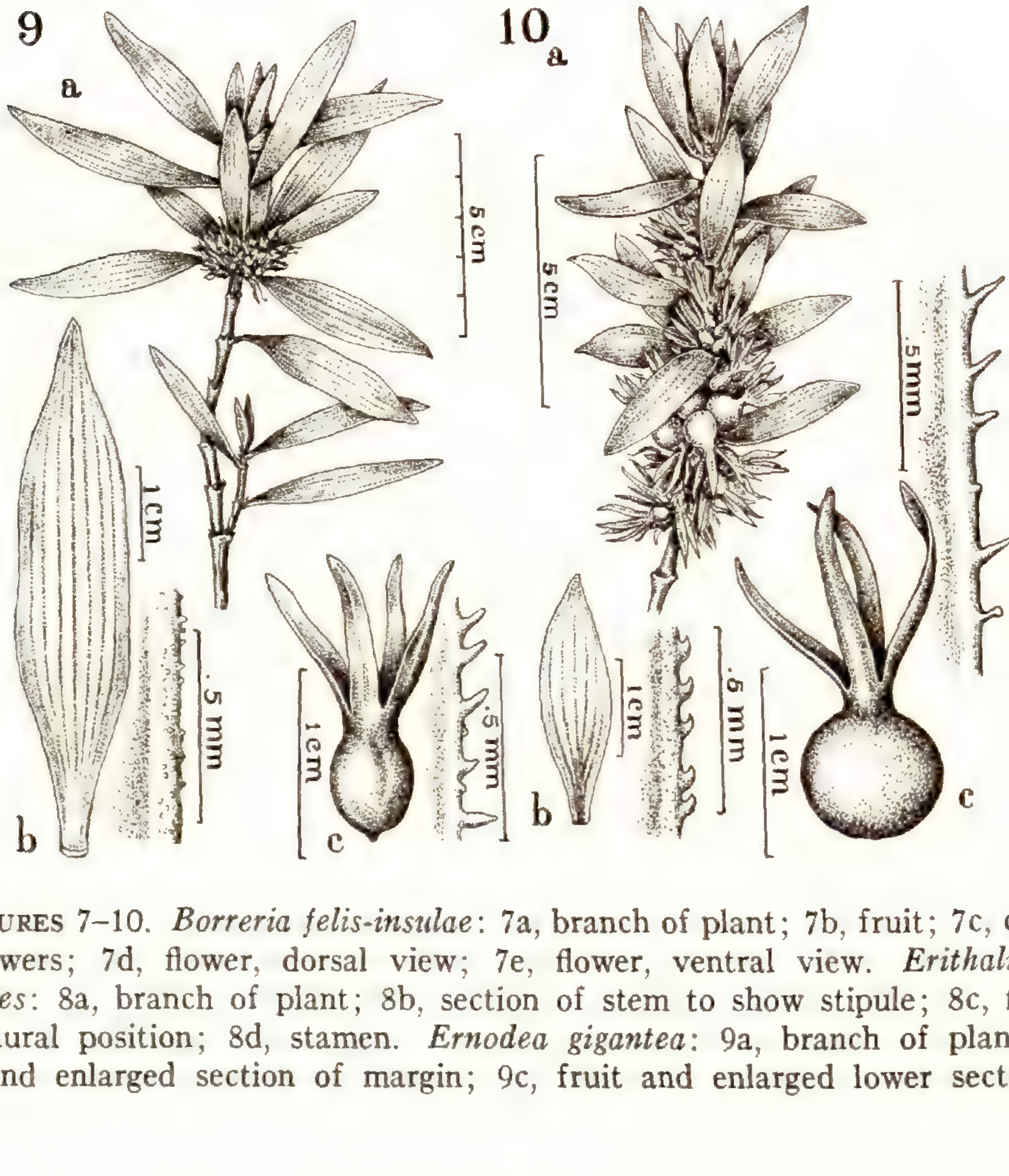
Erithalis diffusa Correll, sp. nov. FIGURE 6.

Frutex diffusus. Ramuli prostrati vel late effusi. Caules subterranei repentes radicantes. Folia coriacea, suborbicularia vel late ovalia, 2–5 cm. longa, 1.5–3 cm. lata. Hypanthium circa 1.5 mm. longum, dentibus rubiginosis, brevibus. Corolla 5–6 mm. longa. Antherae cylindricae, basibus cordiformibus, filamenta gracilia aequantes.

TYPE. Bahamas, San Salvador, in sandy soil of open palm-shrub association just north of airstrip and Teachers College near Riding Rock Point; sprawling shrub with branches prostrate on ground; flowers white; fruits black when ripe, November 21, 1974, *D. S. Correll 43840* (A, holotype; FTG, isotype).

A sprawling shrub with branches prostrate to broadly spreading, rooting where they touch the ground. Stipules connate to form a rounded-truncate, persistent sheath. Leaves coriaceous, suborbicular to broadly oval, broadly rounded at the apex, abruptly tapering or somewhat rounded to the petiole, 2–5 cm. long, 1.5–3 cm. broad; petiole to 1.2 cm. long. Panicles few- to many-flowered, about 5 cm. long, the branches slender. Hypanthium about 1.5 mm. long, the short teeth reddish-brown. Corolla white, 5–6 mm. long, the lobes narrowly elliptic and obtuse. Anthers cylindrical, with cordate bases, 2–2.5 mm. long, about as long as the slender filaments. Fruit orbicular, about 5 mm. in diameter, black when ripe.





FIGURES 7–10. *Borreria felis-insulae*: 7a, branch of plant; 7b, fruit; 7c, cluster of flowers; 7d, flower, dorsal view; 7e, flower, ventral view. *Erithalis salmeoides*: 8a, branch of plant; 8b, section of stem to show stipule; 8c, flower, in natural position; 8d, stamen. *Ernodea gigantea*: 9a, branch of plant; 9b, leaf and enlarged section of margin; 9c, fruit and enlarged lower section of

This plant is characterized primarily by its sprawling growth habit and typically suborbicular leaves. Its long anthers that are the length of their filaments are also distinctive.

Erithalis salmeoides Correll, sp. nov. FIGURE 8.

Frutex compactus globosus, circa 1.5 m. altus. Nodi ramorum apicalium distantes 3–5 mm., plerumque exudatum efferentes. Stipulae connatae vaginam rotundato-truncatam persistentem facientes. Hypanthium 1 mm. longum, ore irregulari rubiginoso. Corolla 2.5–3 mm. longa. Antherae ellipsoideae, circa filamentis filiformibus triple breviores.

TYPE. Bahamas, Great Inagua, in coppice along road between Conch Shell Point and Lantern Head; "balled" shrub 1.5 m. tall; flowers white, August 3, 1975, *D. S. Correll 45897* (A, holotype; FTG, isotype). Topotype: July 23, 1976, *D. S. Correll 47475* (A, F, FTG, NY).

A compact, globose shrub about 1.5 m. tall. Nodes of apical branches 3–5 mm. apart, commonly producing an exudation. Stipules connate to form a rounded-truncate, persistent sheath. Leaves glabrous, coriaceous, obovate to broadly oval, rounded at the apex, abruptly tapering into the short petiole, 1–2.5 cm. long, to about 1.8 cm. wide. Panicles many-flowered, at tips of branches, less than 2 cm. long, the branches short and thick. Hypanthium 1 mm. long, the irregular rim reddish-brown. Corolla white, 2.5–3 mm. long, the lobes oblanceolate and obtuse. Anthers ellipsoid, 0.5 mm. long, about one third as long as the filiform filaments. Unripe fruits orbicular, about 2 mm. in diameter.

This plant bears a remarkable resemblance to *Salmea petrobioides* Grisebach, in the Asteraceae. Its nearest ally appears to be the Cuban *Erithalis vaciniifolia* (Grisebach) Wright ex Sauvalle. In addition to its compact globose habit, it is characterized by having abbreviated internodes, minute flowers, and anthers about one third as long as the filiform filaments.

Ernodea gigantea Correll, sp. nov. FIGURE 9.

Frutex erecto-patens ad 2 m. altus, aspectu laxi-effuso. Rami subquadrangulares, glabrescentes. Folia plus minusve in extremitatibus ramorum, oblique lanceolata vel oblongo-lanceolata, acuta, ad basim sessilem angustata ad 7 cm. longa, 1.5 cm. lata, 5- vel 7-solidinervia, marginibus glabris cartilagineis. Fructus suborbiculares, 5–6 mm. diametro, puberuli vel glabri, in glomerulis certis ad 4 cm. latis. Calycis fructuum lobi oblique lineares, acuti, 7–10 mm. longi, 1–1.5 mm. lati, marginibus ciliolatis vel glabris.

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calyx lobe. *Ernodea serratifolia*: 10a, branch of plant; 10b, leaf and enlarged section of margin; 10c, fruit and enlarged lower section of calyx lobe. *Drawn by Priscilla Fawcett.*

TYPE. Bahamas, Crooked Island, on rock face of hillside cut, just northeast of Cabbage Hill; shrub 2 m. tall, with thick trunk; leaves bunched together at tips of branches; fruits clustered, yellow with a pink color just below calyx lobes, February 22, 1975, *D. S. Correll 44482* (A, holotype; FTG, isotype).

Shrub 2 m. tall, erect-spreading, with a stout, simple main stem to about 1 cm. thick and with lax, open growth. Branches subquadrangular, the young ones puberulent, eventually becoming glabrous. Stipules trilobulate, the central linear lobule elongate. Leaves more or less clustered near ends of branches, obliquely lanceolate to oblong-lanceolate, acute, narrowed to the sessile base, to 7 cm. long and 1.5 cm. wide, with 5 to 7 veins, the margins minutely papillose or smooth and cartilaginous. Fruits numerous, in dense, well-defined glomerules as much as 4 cm. across. Flowers not seen but said to be orange-red. Fruits suborbicular, 5–6 mm. in diameter, puberulent or glabrous. Calyx lobes on fruits obliquely linear, acute, 7–10 mm. long, 1–1.5 mm. wide, the margins ciliolate or glabrous.

All seven of the species that comprise this genus are found in our region. The genus has had no serious attention since N. L. Britton's revision in 1908 (Bull. Torrey Bot. Club **35**: 203–208). In addition to describing three new species in this work, Britton designated several Bahamian collections as "Races" under the widespread *E. littoralis* Swartz. Two of these so-called "Races" that I have collected and studied are here described as entirely new taxa.

Ernodea gigantea, as its name implies, is the largest member of this genus. In its erect habit and thick main stem, it differs markedly from the usually weak-stemmed, sprawling plants that make up this genus. In addition, its well-defined, densely glomerate inflorescence, large leaves, and unusually long calyx lobes are distinctive.

This species is apparently confined to Crooked Island as evidenced by the following additional collections: Long Cay, road to South Side, December 7–17, 1905, *L. J. K. Brace 4069* (US); road to Stopper Hill, January 9–23, 1906, *L. J. K. Brace 4807* (US); low-lying land near mangroves on west side of island along road from Church Grove to boat landing, flowers orange-red, April 20, 1971, *William T. Gillis 10618* (FTG).

Ernodea serratifolia Correll, sp. nov. FIGURE 10.

Frutex erecto-patens ad 1.5 m. altus, aspectu denso. Folia in ramis remota, elliptica vel lineari-lanceolata pungentia, ad basim sessilem decrescentia, ad 4.5 cm. longa, 1 cm. lata, 5- vel 7-solidinervia, marginibus serrulatis. Fructus numerosi, lutei, orbiculares, 6–7 mm. diametro, puberuli vel glabri, in glomerulis indefinitis. Calycis fructuum lobi lineares, acutocuspidati, 8–12 mm. longi, 1.5–2.5 mm. lati, marginibus serratis vel glabris.

TYPE. Bahamas, Great Inagua, in open, gravelly flat at east end of Matthew Town airstrip; spreading shrub about 1.5 m. tall; fruits numer-

ous, yellow, July 19, 1976, *D. S. Correll 47396* (A, holotype; FTG, isotype). Topotype: August 4, 1975, *D. S. Correll 45910* (A, F, FTG, NY).

Shrub erect-spreading to 1.5 m. tall, with rather dense habit of growth. Branches and branchlets quadrangular, the younger ones puberulent. Stipule with several teeth, the linear central one much elongate. Leaves scattered on the branches, elliptic to linear-lanceolate, pungently acute, tapering to the sessile base, to 4.5 cm. long and 1 cm. wide, 5- or 7-veined, the margins serrulate with cartilaginous teeth. Flowers not seen. Fruits numerous along the branches, yellow, orbicular, 6–7 mm. in diameter, puberulent or glabrous. Calyx lobes on fruits linear, acute-cuspidate, 8–12 mm. long, 1.5–2.5 mm. wide, the margins serrulate or smooth.

This species is most closely allied to *Ernodea gigantea*. The smaller, permanently serrulate leaves and somewhat different growth habit, however, would appear to separate it from that species. The plant occurs commonly on Great Inagua where a number of sites were noted, but was not seen on Little Inagua.

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SARGENT'S FIR HYBRID: ABIES AMABILIS × LASIOCARPA

WILLIAM B. CRITCHFIELD

ON A SHORT TRIP into the northern Olympic Mountains of Washington in the summer of 1896, Professor Charles Sprague Sargent found a fir tree that he thought might be a natural hybrid between *Abies amabilis* (Dougl.) Forbes and *A. lasiocarpa* (Hook.) Nutt. The founder and Director of the Arnold Arboretum, Sargent was generally recognized as America's pre-eminent dendrologist. His brief description of the putative hybrid (Sargent, 1898) is still the only report of natural hybridization between *A. amabilis* and any of the firs with which it grows (Klaehn & Winieski, 1962). On the same trip Sargent encountered a tree that he identified as *A. nobilis* (Dougl.) Lindley (since renamed *A. procera* Rehd.). His report that this species grew in the Olympic Mountains persisted in the literature of botany and forestry for many years before it was dropped for lack of confirmation. In this paper the identity of these firs is reexamined, and the unusual circumstances of their collection is reviewed.

Sargent visited the Olympic Peninsula in his official capacity as chairman of a blue-ribbon committee charged with formulating a policy for the federal forest lands of the United States. The committee was appointed by the President of the National Academy of Sciences at the request of the Secretary of the Interior, and was in existence from early 1896 to mid-1897. The group lacked a formal name, but has most commonly been called the National Forest Commission ("U. S. Forestry Commission" on Sargent's printed herbarium labels). Most of the Commission members were elder statesmen of American science and members of the National Academy. The only exception was Gifford Pinchot, who was on the Commission at Sargent's request. Pinchot was one of the few professionally trained foresters in the country, and later became the first head of the Forest Service.

Between early July and late October of 1896, Sargent and most of the other Commission members visited the forested regions of the West. An unofficial member of the party was the naturalist John Muir (Badè, 1923). Except for Pinchot, who set out for the West a month earlier and joined the others only intermittently (Pinchot, 1972), they traveled as a group.

The recommendations of the Commission focused national attention on the forests of the public domain for the first time, led to more than doubling the area in Forest Reserves, and influenced the timing and content of the Organic Act of 1897. The continuing importance of the Organic Act was demonstrated in 1975, when it provided the legislative basis for the Monongahela decision concerning timber-harvesting practices on eastern National Forest lands (U. S. Court of Appeals, 4th Circuit, 1975).

Considering the lasting significance of the Commission's work, remark-

ably little is known about its western journey. If Sargent kept journals or field books, they have not survived (S. B. Sutton, personal communication). John Muir's published letters place the Commission in the Black Hills of South Dakota in early July, at the start of the trip, and in southern Oregon in late August, after they had visited western Washington (Badè, 1923; Wolfe, 1938). Pinchot's autobiography gives a fairly detailed account of his travels, but he did not accompany the others to Washington. He left them in Montana some time in late July and rejoined them — probably in Portland, Oregon — for the train trip south to Ashland, where they arrived on August 26 (Pinchot, 1972; U. S. Senate, 1897).

The only published mention of the Commission's whereabouts between late July and late August is Sargent's footnote concerning the putative hybrid fir (Sargent, 1898, p. 126): "On a ridge of the Olympic Mountains separating the waters of the Solduc from those of the Quillyhute, I found, on August 19, 1896, at an elevation of four thousand five hundred feet above the sea, an Abies sixty to eighty feet in height, growing with *Abies lasiocarpa* and *Abies amabilis*, with the slender spire-like head and the foliage of the former and the cones of the latter. It was, perhaps, a natural hybrid between those species."

In 1896 the Olympic Peninsula was still one of the least explored parts of the country. The *Seattle Press* and O'Neil expeditions had penetrated the mountainous interior only six years earlier, and the highest point on the peninsula (the West Peak of Mt. Olympus) may not have been climbed until 1907 (El Hult, 1954). Only months before the Commission's trip, the first reasonably good map of the interior was published in the April issue of *National Geographic Magazine* (Gilman, 1896).

The Commission's trip into the Olympics seems to have been overlooked by local historians, although the ridge where Sargent may have collected his putative hybrid is deep in the mountains. El Hult (1954), whose account of the exploration of the Olympics extends through 1907, does not mention the Commission. Piper (1906) does not list either Sargent or the Commission among the plant collectors on the Olympic Peninsula through 1903, nor does Jones (1936) in his survey of the botanical exploration of the peninsula.

Sargent's published note and specimen labels (in the herbarium of the Arnold Arboretum) do not mention his companions on the expedition into the Olympics. One likely candidate is Commission member Arnold Hague of the U. S. Geological Survey, who was the same age as Sargent (55). John Muir would certainly have made the trip if he was with the Commission in Washington. The other two Commission members on the western trip, Professor William H. Brewer of Yale University and General Henry L. Abbot of the Army Engineers, were much older than the others and less likely to have taken part in what must have been an arduous expedition.

Sargent and his companions must have followed the Soleduck River into the mountains. The small tree that he identified as *A. nobilis* was growing near "the Solduck River at an elevation of three thousand feet"

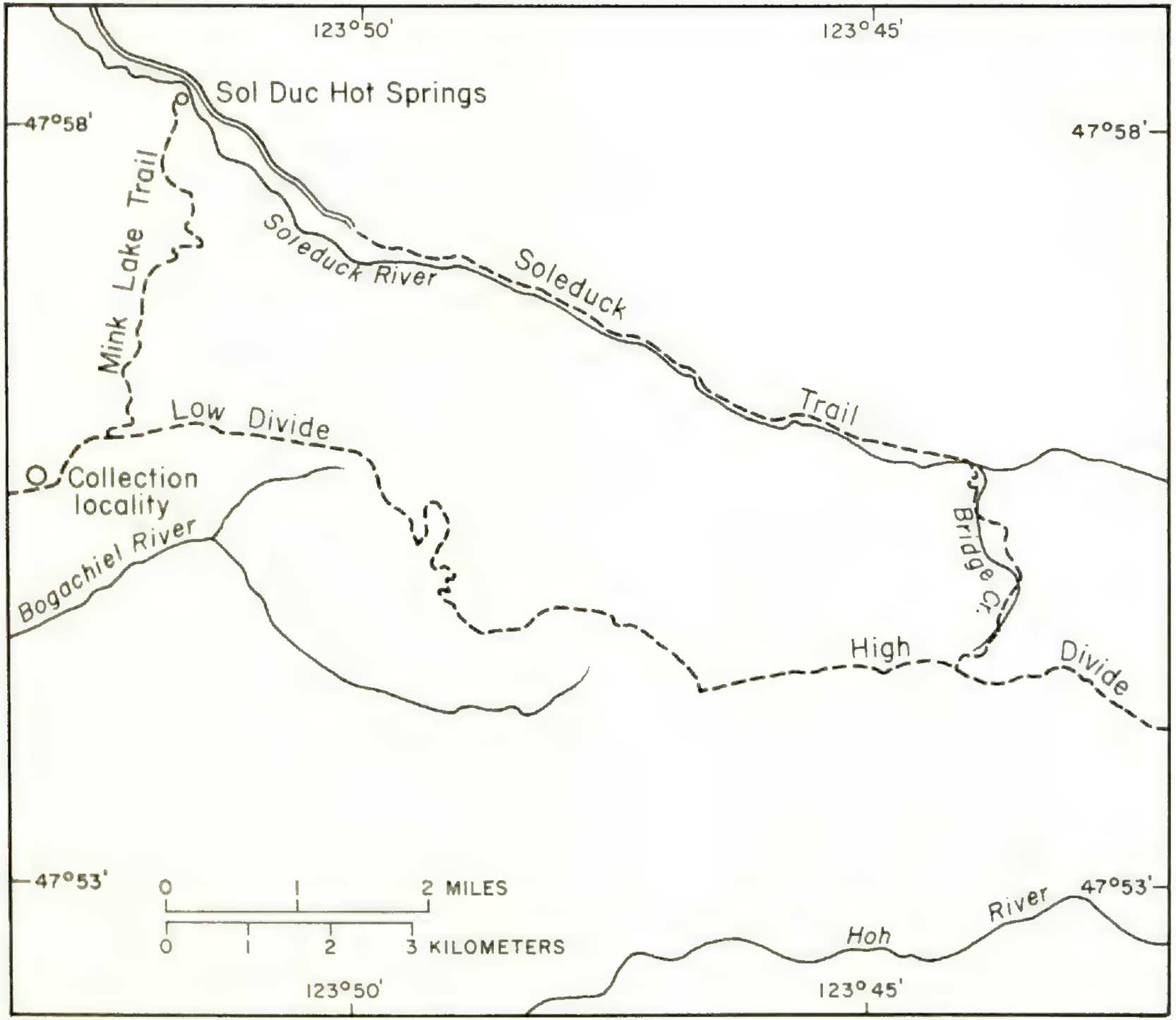
(Sargent, 1898, p. 134). The map accompanying the Dodwell-Rixon forest survey of 1899 (U. S. Geological Survey, 1900) shows a wagon road or well-marked trail along the Soleduck River as far as the vicinity of Sol Duc Hot Springs, near the end of the present road (MAP 1). Their report noted that a traveled trail extended beyond this point to the head of the Soleduck River (U. S. Geological Survey, 1900, p. 158). If this trail existed three years earlier, it is probably the route that Sargent and his party followed.

One puzzling feature of Sargent's hybrid is its location. His description — a ridge between the Soleduck and Quillayute drainages — was a geographical impossibility even in 1896. The name "Quillayute River" is, and apparently always has been, restricted to the short stretch of river between the confluence of the Soleduck and Bogachiel rivers and the river mouth on the Pacific Ocean. The Quillayute, Bogachiel, and Soleduck rivers all have their present names (with variations in spelling) and locations on Gilman's map (Gilman, 1896) and earlier maps I have seen. The ridge Sargent referred to is probably either the Low Divide, which separates the headwaters of the Bogachiel River from the Soleduck drainage, or the High Divide, between the headwaters of the Soleduck and the major drainage of the Hoh River (MAP 1).

The Low Divide is the less likely of the two, even though the Bogachiel River is part of the system that ultimately forms the Quillayute River. In 1896 the Low Divide may have been much more difficult to reach than the High Divide. The first evidence of trail access from the Soleduck River is a 1912 map of the Olympic National Forest (on file at the Forest Supervisor's Office in Olympia) showing the Mink Lake trail to the Low Divide. At the end of this trail, the Low Divide is mostly below the lower limits of *Abies lasiocarpa*. However, that species and *A. amabilis* occur together on a 4300 foot knoll on the Low Divide about a mile west of the Mink Lake trail (MAP 1). In 1970 I collected bark resin and foliage from both species in this grove. None of the trees showed any indication of intermediacy in either morphology or resin composition (Zavarin *et al.* 1973).

The High Divide is the most likely candidate for the ridge where Sargent collected his hybrid, although the elevation is 500 to 600 feet higher than Sargent's estimate of 4500 feet. The High Divide is only a few hundred yards from the head of Bridge Creek, one of the headwaters of the Soleduck River. Bridge Creek is still the only headwater stream accessible by trail, and the only one with a nearby ridge separating major drainages.

The High Divide must have been fairly accessible by 1897, two years before Dodwell and Rixon mentioned a trail to the head of the Soleduck. In August, 1897, just a year after the Commission was in the Olympics, Gifford Pinchot visited the Olympic Forest Reserve as Confidential Forest Agent for the U. S. Department of the Interior. By chance, at Lake Crescent, he encountered Dr. C. Hart Merriam, head of the U. S. Department of Agriculture's Division of Biological Survey. Pinchot and Merriam, together with a local woodsman named Blackwood, retraced Sargent's



MAP 1. A portion of the northern Olympic Mountains, Washington.

probable route, traveling "by way of Soleduck Hot Springs to the Hoh River divide, from which the view of Mt. Olympus was beyond description" (Pinchot, 1972). Merriam apparently turned back at that point, but Pinchot and Blackwood descended from the High Divide into the Bogachiel River drainage and followed the river back to civilization. Pinchot thought it was possible that he and his companion were the first white men in the upper Bogachiel drainage, and he may have been right; El Hult (1954) records no earlier exploration of the area.

Although the location of Sargent's hybrid cannot be established with certainty, the specimen he collected is in the herbarium of the Arnold Arboretum, and I have checked its identity. The discrepancies between the specimen and Sargent's published description of the tree (quoted in full above) raise the question of why Sargent thought this tree might be a hybrid.

The leaves on vegetative and male branches of *Abies lasiocarpa* and *A. amabilis* are most reliably identified by stomatal distribution, orientation, and resin canal location, but shape is also helpful. The rather uniform leaves of *A. amabilis* have a well-defined notch at the tip and a deep groove in the upper surface from the notch to the base. The extremely variable leaves of *A. lasiocarpa* usually have a less well-defined groove, and the tip may be rounded, pointed, or notched. Stomata are present on both surfaces of the leaves of this species. On *A. amabilis* leaves they are usually restricted to the abaxial surfaces, but sometimes the adaxial surfaces are stomatiferous near the notch. Leaf orientation is strikingly different in the two firs: the adaxial surfaces of *A. lasiocarpa* leaves are oriented in varying planes, but the green, stomata-free, adaxial surfaces of *A. amabilis* leaves face upward. They achieve this orientation by a sharp twist at the leaf base. *Abies lasiocarpa* is the only Northwestern fir with medial resin canals in the leaves; in *A. amabilis* the canals are external and adjacent to the abaxial epidermis.

Cone and seed characteristics are not too helpful in identifying these firs, although the cones of *Abies amabilis* are usually larger in all dimensions than those of *A. lasiocarpa*. One fairly reliable distinction is the shape of the bract subtending the cone scale. In *A. lasiocarpa*, the bract narrows abruptly to a point 2–3 mm. long, and in *A. amabilis* it narrows gradually to a point about the same length. The wings of *A. amabilis* seeds are straw-colored (Harlow & Harrar, 1941), and usually lack the flecks and streaks of pigment that give the seed-wings of *A. lasiocarpa* their darker color.

Sargent's specimen includes vegetative branches, branches with staminate strobili, and separately packaged cones. On the labels Sargent noted that the cones are like *Abies amabilis* and the foliage is like *A. lasiocarpa*. The collection date on the labels is August 18, 1896, a day earlier than the published date. The leaves on both kinds of branches correspond to *A. amabilis* in all respects: shape, stomatal distribution, orientation, basal twist, and position of resin canals. The cones, which had probably reached their final size by August 18 or 19 (see Franklin & Ritchie, 1970), are intermediate in size — large for *A. lasiocarpa* and small for *A. amabilis*.

Three detached (and possibly incomplete) cones are 8.5–8.8 cm. long. The single cone still attached to the branch is 10.5 cm. long, at the lower end of the size range of *A. amabilis* cones. The cone bracts have gradually tapered points like *A. amabilis*, and the nearly mature seeds have the straw-colored wings of *A. amabilis*. Included with the cones is this note dated June 24, 1913, by W. H. Lamb, a student of the western firs (Lamb, 1912): "An examination of the cone-bracts and the position of the resin ducts in the leaves will show that these specimens are all *Abies amabilis*, and not of hybrid origin."

A few years after Sargent's note appeared in print, Masters (1901, *fig. 26*) published illustrations of the putative hybrid, entitled "Professor Sargent's hybrid *Abies*." Masters quoted Sargent's published note without comment, but the sketches clearly portray leaves of *A. amabilis*. The upper and lower surfaces of a leaf (Masters, *fig. 26C*) show the notched tip and basal twist, and a leaf transection (Masters, *fig. 26E*) shows the external resin canals of *A. amabilis*. The crudely drawn bracts (Masters, *fig. 26A, B*) are completely unlike those of *A. lasiocarpa*. They lack a long, well-defined point, and might possibly fall within the range of variation of *A. amabilis*.

Although the specimen Sargent labeled a putative hybrid is *Abies amabilis*, his field observation of a tree with intermediate characteristics cannot be disregarded. In the late summer of 1896, he was particularly familiar with the distinguishing characteristics of the western firs. He must have just recently completed the text of Volume XII of "Silva of North America" dealing with *Abies* and related genera; his comments on the firs of the Olympic Mountains were added as footnotes before the book was printed in 1898. And, just before the trip into the Olympics, the Commission probably had seen all of the northwestern firs in the Cascade Mountains of Washington.

Abies lasiocarpa and *A. amabilis* have abundant opportunities to cross in nature. They grow together in many places in the mountains of the Pacific Northwest, and overlap in flowering time (Ebell & Schmidt, 1964; Franklin & Ritchie, 1970). In its resin composition (Smedman *et al.*, 1969; Zavarin *et al.*, 1973) and morphology, *A. amabilis* has no close affinities with the other American firs. It is usually classified with *A. concolor* (Gord. & Glend.) Lindley and *A. grandis* (Dougl.) Lindley, primarily because of the external location of the leaf resin canals, but it also resembles *A. lasiocarpa* and its relatives in some respects (Zavarin *et al.*, 1973). We have looked for evidence of chemical and morphological intermediacy in mixed stands in the Olympic Mountains, as noted earlier, and in the Oregon Cascades, but so far without success.

The other puzzling collection made by Sargent on the trip into the Olympics is the *Abies procera* tree he found near the Soleduck River, the only *A. procera* ever reported on the Olympic Peninsula. Although he saw no other trees of this species on the trip, he considered its presence in the Olympics confirmed: "the following year this species was seen by Dr. C. Hart Merriam in the same region" (Sargent, 1898, p. 134). Sargent may

have been referring to an observation made on Merriam's 1897 trip with Gifford Pinchot up the Soleduck drainage to the High Divide.

Sargent's extension of the range of *Abies procera* to the Olympic Mountains was quoted by Piper (1906), and enlarged on by Sudworth (1908): "North side of Olympic Mountains on Solduck River, at about 3,000 feet, and general at higher elevations." Munns (1938, *Map 46*) further expanded the distribution to a broad band of *A. procera* around the high-mountain core of the peninsula. However, Jones (1936), in his botanical survey of the peninsula, pointed out the lack of recent evidence that *A. procera* grows there. The last published report of this fir in the Olympics appears to be Little's 1949 map showing a limited distribution in the northern part of the peninsula (Little, 1949, *Map 133*).

The vegetative specimen labeled "*Abies nobilis*," collected on the same day as the putative hybrid, is *A. lasiocarpa* rather than *A. procera*. The leaves are flattened, not quadrangular in section; the groove on the upper surface is broad and ill-defined rather than narrow and sharply defined, and the resin canals are medial, not external as in *A. procera*. Sargent's estimate of 3000 feet is very low for *A. lasiocarpa* in the Olympic Mountains. However, he noted on the label that the tree was growing on the bank of the Soleduck River, and it is not uncommon for montane trees to occur along streams well below their usual elevational range.

How did Sargent happen to mislabel or misidentify these two important collections from the Olympic Peninsula? The explanation probably lies in the hectic schedule of the Commission on its western journey. Sutton (1970) notes that Sargent "collected specimens furiously all along the way, lugging his increasingly cumbersome possessions with him as the party sped from one place to the next." These difficult circumstances may explain Sargent's identification of *Abies lasiocarpa* as *A. procera* and his labeling of an *A. amabilis* specimen as a putative hybrid.

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GOMPHRENOIDEAE (AMARANTHACEAE) OF THE BAHAMA ISLANDS

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THIS PAPER IS PRESENTED to clarify the identity and nomenclature of members of the Gomphrenoideae represented in the Bahama Islands, including the Turks and Caicos Islands. The Gomphrenoideae have been the special study of the first author for several years; the Bahama flora is under revision by the second author and George R. Proctor.

In the Amaranthaceae, members of the subfamily Gomphrenoideae are characterized by anthers with two chambers, i.e., with a single longitudinal line of dehiscence. The other genera of the Amaranthaceae (*Amaranthus*, *Achyranthes*, *Celosia*) in the flora of the Bahamas have four-chambered anthers with two longitudinal lines of dehiscence, and are members of subfamily Amaranthoideae.

Four genera of the Gomphrenoideae have been collected in the Bahamas: *Alternanthera*, *Iresine*, *Lithophila*, and *Philoxerus*. *Alternanthera* Forssk. was called *Achyranthes* L., while *Achyranthes* L. was called *Centrostachys* L. by Britton and Millspaugh (1920), following Standley (1915). In 1920 eight species of Gomphrenoideae were reported. We report nine species, with only three names in common with the earlier flora. Two other names are considered synonyms, and one additional species is reported. Five other widespread species of the Gomphrenoideae may possibly be found in the flora, but have not been collected so far as we know. Specimens identified by various botanists as *Achyranthes aspera* L., *Celosia nitida* Vahl, and six species of *Amaranthus* have been seen from the Bahamas, but are not treated in this paper in which only members of the Gomphrenoideae are considered.

KEY TO THE GENERA OF GOMPHRENOIDEAE IN THE BAHAMAS

(Names indicated in parentheses represent taxa not yet found in the Bahama Islands, which are weedy or frequent escapes from cultivation, and may yet appear within the archipelago.)

A. Inflorescences diffuse, most flowers unisexual. ..... *Iresine*.

A. Inflorescences globose, flowers hermaphroditic.
  B. Stigma capitate to bilobed. ..... *Alternanthera*.
  B. Stigma bifid or trifurcate and attenuate.
    C. Filaments with fimbriate lateral processes atop the tube. ..... (*Gomphrena*).
    C. Filaments ligulate, with a shallow cup.
      D. Fertile anthers 5, staminodes absent; leaves spread along stem. ..... *Philoxerus*.

D. Fertile anthers 2, staminodes 3, longer leaves in basal rosettes. ..... *Lithophila*.

Alternanthera Forsskål, Fl. Aegypt.-Arab. 28. 1775.

Mogiphanes Martius, Nov. Gen. Sp. **2:** 29. *t. 129.* 1826.
Telanthera R. Brown in Tuckey, Narr. Congo 447. 1818.
Achyranthes sensu Standley, Jour. Wash. Acad. Sci. **5:** 74. 1915, non L.

Key to the Species of Alternanthera in the Bahamas

A. Inflorescences terminal, pedunculate. ..... 5. *A. brasiliana.*
A. Inflorescences axillary, sessile.
  B. Pseudostaminodia mostly ligulate.
    C. Calyx lobes acute but not spinescent, subglabrous with simple trichomes.
      D. Mature fruit strongly bilaterally symmetrical, inflated, expanding beyond the calyx. ..... (*A. sessilis*).
      D. Mature fruit slightly bilaterally symmetrical, not inflated, included within calyx. ..... 2. *A. paronychioides.*
    C. Calyx lobes spinescent, pubescent with glochidiate barbed trichomes.
      E. Largest leaves about 2 cm. long by 2 cm. wide; calyx lobes usually more than 4 mm. long, strongly spinescent. ..... (*A. pungens*).
      E. Largest leaves about 1.5 cm. long by 1 cm. wide; calyx lobes usually less than 4 mm. long, spinescent. ... 1. *A. caracasana.*
  B. Pseudostaminodia fimbriate.
    F. Calyx glabrous, leaves ± sessile. ..... 3. *A. maritima.*
    F. Calyx pubescent, leaf petioles conspicuous.
      G. Leaves obtuse, with very dense stellate pubescence. ..... 4. *A. canescens.*
      G. Leaves acute, with very little pubescence, trichomes simple. ..... (*A. tenella*).

1. **Alternanthera caracasana** HBK. Nov. Gen. Sp. **2:** 205 [folio ed.]. 1818.

Alternanthera villiflora Scheele, Linnaea **22:** 149. 1849.
Alternanthera achyrantha parvifolia Moquin in DC. Prodr. **13**(2): 359. 1849.
Alternanthera peploides (Willd. ex Roemer & Schultes) Urban, Repert. Sp. Nov. **15:** 168. 1918.
Alternanthera macrorhiza Hauman, Bull. Jard. Bot. Brux. **18:** 114. 1946.

This species was called *Achyranthes repens* L. by Britton and Millspaugh (1920), but *Achyranthes repens* L. is a synonym of *Alternanthera pungens* HBK. [= *Alternanthera repens* (L.) Smith, 1818, non *Alternanthera repens* J. F. Gmelin, 1791]. It is known as "washerwoman" in the Bahamas.

2. **Alternanthera paronychioides** St. Hil. Voy. Brés. 2(2): 43. 1833.

Gomphrena Ficoidea L. Sp. Pl. ed. 1. 1: 225. 1753.
Alternanthera ficoidea (L.) Smith in Rees, Cyclop. Vol. 39 [Addend. & Corrig., alph. ord.]. 1818 [1819]. [non *Alternanthera ficoides* Palisot de Beauvois, 1818 = *Alternanthera sessilis* (L.) DC.]
Alternanthera pilosa Moquin in DC. Prodr. 13(2): 357. 1849.
Alternanthera chacoensis Morong, Ann. New York Acad. Sci. 7: 208. 1893.
Alternanthera felipponei Beauverd, Bull. Soc. Bot. Genève. Ser. 2. 1921: 268. 1922.

This species was called *Achyranthes polygonoides* (L.) Lamarck by Britton and Millspaugh (1920), but the basionym, *Gomphrena polygonoides* L., 1753, is a *nomen dubium* (Pedersen, 1967) and must be avoided. It is a surprise to us that *Gomphrena ficoidea* L., 1753, belongs here, for it had been identified with the taxon originally described as *Bucholzia polygonoides* γ *diffusa* Martius, 1826, until J. F. Veldkamp (pers. comm.) examined van Royen's specimen in Leiden. The choice of names for this species is replete with subjective decisions (Pedersen, 1967) and will be discussed by the senior author in another paper.

3. **Alternanthera maritima** (Martius) St. Hil. Voy. Brés. 2(2): 43. 1833.

Britton and Millspaugh called this species *Achyranthes maritima* (Martius) Standley. It is found chiefly on beaches of islands on the Great Bahama Bank, but also occurs in maritime tropical Brazil and West Africa.

4. **Alternanthera canescens** HBK. Nov. Gen. Sp. 2: 204, 205 [folio ed.]. 1818, non (HBK.) Moquin, 1849 = *Iresine canescens* H. & B. ex Willd. 1806.

Alternanthera forsstroemii Fries, Ark. Bot. 16(12): 12. 1921.
Alternanthera crassifolia (Standley) Alain, Contr. Ocas. Mus. Hist. Nat. Col. "De la Salle" 9: 1. 1950.
Achyranthes crassifolia Standley, Proc. Biol. Soc. Wash. 32: 241. 1919.

During a research visit to the island of Grand Turk in 1974, Gillis and Proctor collected an unknown *Alternanthera* in *Acacia* thorn-scrub between the townsite and the airport. Mears has determined this collection as *A. canescens* HBK.

Gillis & Proctor 12186 is the first collection of this species in the Bahama Archipelago, and is the first collection from north of the Venezuelan coastal islands of sufficient material for analysis. The two collections from Guadeloupe and Cuba, types of the Fries and Standley names, have been too incomplete for certain identification. The Gillis and Proctor material demonstrates that *Alternanthera canescens* HBK. does occur on West Indies islands, and indicates that the Fries and Standley species were insufficiently distinct to warrant their separation as species. The Gillis and Proctor specimens are deposited at A and IJ.

5. **Alternanthera brasiliana** (L.) Kuntze, Rev. Gen. Pl. 2: 537. 1891.

Gomphrena brasiliana L. Centuria II: 135. 1756.
Philoxerus brasiliana (L.) Smith in Rees, Cyclop. Vol. 27. [alph. ord.]. 1814.
Alternanthera jacquinii (Schrader) Grisebach ex Kuntze, *op. cit.* 538. 1891, *pro syn.*
Alternanthera straminea (Martius) Millspaugh, Field Mus. Bull. **1**: 39. 1932, non Stuchlik, 1913, *sphalm.*

The limit of the type variety is complex and will be elaborated upon by the first author in a separate paper. The type variety of this species is found throughout the Caribbean and in northern South America, extending into Brazil. This species was collected for the first time in the Bahamas on Long Island by Steven R. Hill (Hill, 1974). The second author has also gathered it from a ruderal site on New Providence Island.

There are three other taxa of *Alternanthera* which are found nearly throughout the Caribbean, but which have not yet been collected in the Bahamas: *Alternanthera sessilis* (L.) DC., *A. pungens* HBK. [= *A. repens* (L.) Smith, *A. achyrantha* (L.) R. Br. ex Roemer & Schultes], and *A. tenella* Colla.

Gomphrena L. Sp. Pl. ed. 1. 1: 224. 1753; Gen. Pl. 105. 1754.

It is possible that *Gomphrena globosa* L., 1753, and *G. serrata* L., 1753 (= *G. decumbens* Jacquin, 1805, *G. dispersa* Standley, 1916) occur in the Bahamas from time to time as escapes from cultivation, inasmuch as they do so elsewhere in the West Indies. No specimens have yet been found, however. *Gomphrena globosa* has capitula greater than 1.5 cm. in diameter, usually brightly colored, with large, ovate-acute leaves. *G. serrata* has capitula less than 1.2 cm. in diameter, usually white to pink, with leaves lanceolate-acute to obtuse.

Iresine P. Browne, Hist. Jamaica 358. 1756.

Rosea Martius, Nov. Gen. Sp. **2**: 58. 1826.
Trommsdorffia Martius, *ibid.* 40. *t. 136.*
Ireneis Moquin in DC. Prodr. **13**(2): 349. 1849.

KEY TO THE SPECIES OF IRESINE IN THE BAHAMAS

Leaves ovate-lanceolate, acute; inflorescence diffusely paniculate. . *I. canescens.*
Leaves elliptic-linear, rounded; inflorescence narrow. ..... *I. flavescens.*

1. **Iresine canescens** Humboldt & Bonpland ex Willdenow, Sp. Pl. ed. 4. **4**: 765. 1806.

Celosia paniculata L. Sp. Pl. ed. 1. **1**: 206. 1753.
Iresine paniculata (L.) Kuntze, Rev. Gen. Pl. **2**: 542. 1891, non Poir. 1814.
Iresine Celosia L. Fl. Jam. 1758 and Syst. ed. 10. 1291. 1759, *nomen illegit.*
Iresine celosioides L. Sp. Pl. ed. 2. **2**: 1456. 1763, *nomen illegit.*
Iresine elongata Humboldt & Bonpland ex Willd. *op. cit.* 765. 1806.

Alternanthera dubia HBK. Nov. Gen. Sp. **2:** 209 [folio ed.]. 1818.
Iresine parvifolia HBK. *ibid.* 198.
Iresine havanensis HBK. *ibid.* 199.
Iresine polymorpha Martius, Nov. Gen. Sp. **2:** 56. *t. 153.* 1826.
Trommsdorffia canescens (H. & B. ex Willd.) Martius, *ibid.* 42.
Iresine floribunda Martens & Galeotti, Bull. Acad. Brux. **10:** 347. 1843.
Iresine gracilis Martens & Galeotti, *ibid.* 347.
Iresine frutescens Moquin in DC. Prodr. **13**(2)**:** 344. 1849.

This is the type species of *Iresine* and one of the most widely distributed species of Amaranthaceae. *Celosia paniculata* L., 1753, is well typified and is clearly this species but cannot be transferred to *Iresine* because the name *Iresine paniculata* Poir., 1814, is a synonym of *Iresine angustifolia* Euphrasén, 1798. When Linnaeus named *Iresine Celosia* L., 1758, and *Iresine celosioides* L., 1762, placing them in his class DIOECIA PENTANDRIA, he cited *Celosia paniculata* L., 1753, and refrained from listing *Celosia paniculata* separately. He simply transferred *Celosia paniculata* to P. Browne's *Iresine* when he discovered it was dioecious. The earliest valid name in *Iresine* is *I. canescens.*

2. **Iresine flavescens** Humboldt & Bonpland ex Willdenow, Sp. Pl. ed. 4. **4:** 766. 1806.

Alternanthera flavescens (Humboldt & Bonpland ex Willd.) Moquin in DC. Prodr. **13**(2)**:** 350. 1849, non HBK., 1818.
Iresine inaguensis Millspaugh, Publ. Field Mus. Bot. **2:** 149. 1906.
Iresine keyensis Millspaugh, *ibid.* 148.

This species is endemic to the West Indies and was included in the previous flora under this name. *Iresine inaguensis* might be distinguished as a form with linear, nearly sessile leaves, found from Castle Island and Samana Cay southward in the archipelago (see FIGURE 1).

Lithophila Swartz, Prodr. 14. 1788.

1. **Lithophila muscoides** Swartz, *ibid.*

Alternanthera caribaea Moquin in DC. Prodr. **13**(2)**:** 354. 1849.
Alternanthera muscoides (Sw.) Hook. f. in Benth. & Hook. f., Genera Pl. **3:** 39. 1883.
Iresine muscoides (Sw.) Kuntze, Rev. Gen. Pl. **1:** 542. 1891.

This species, commonly found on coastal muds and on the shores of brackish ponds throughout the archipelago, becomes more common in the drier islands to the south.

Philoxerus R. Brown, Prodr. 416. 1810.

1. **Philoxerus vermicularis** (L.) Smith ("-atus") in Rees, Cyclop. vol. 27. [alph. ord.]. 1814.

Gomphrena vermicularis L. Sp. Pl. **1:** 224. 1753.

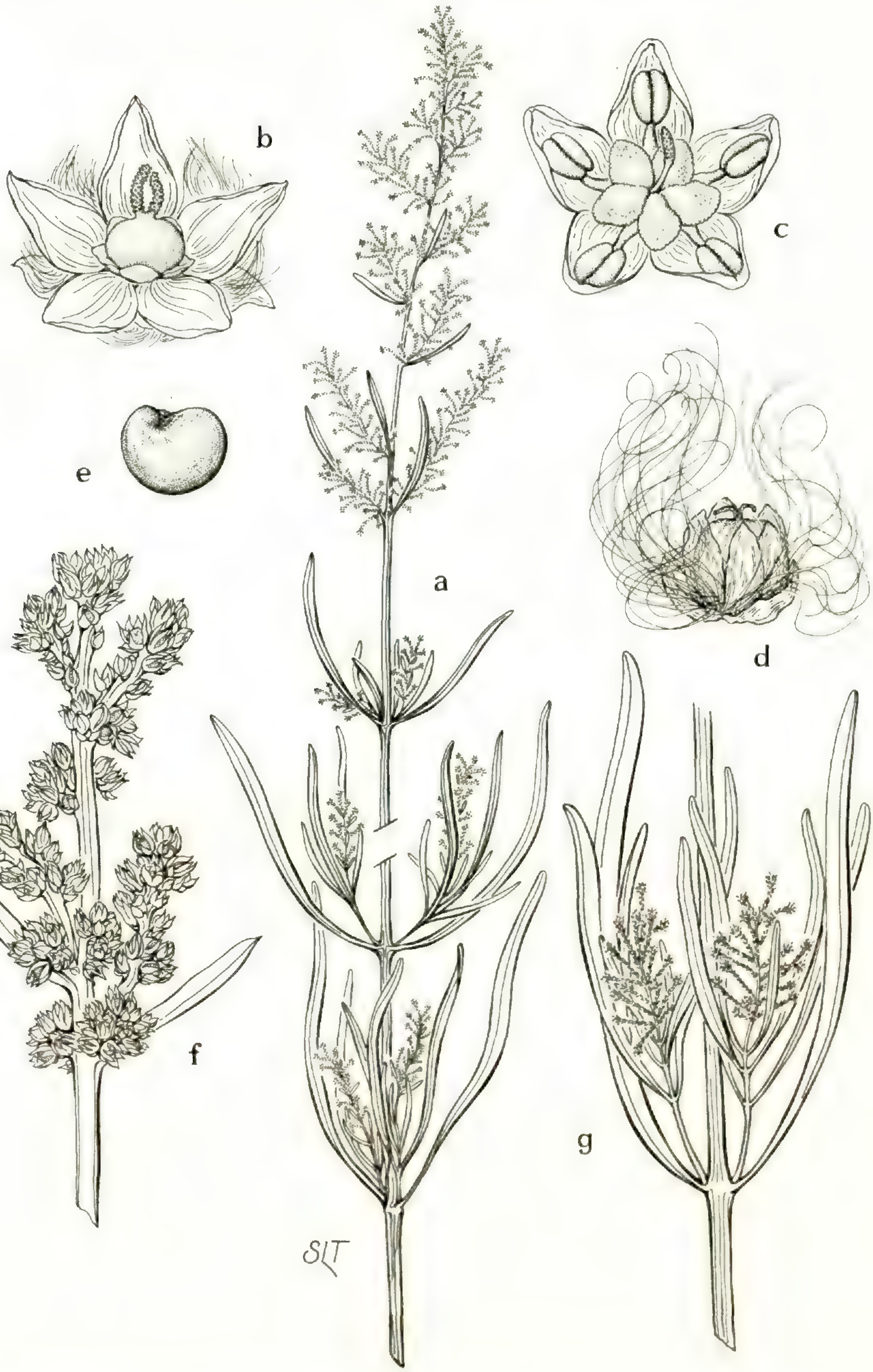

FIGURE 1. *Iresine flavescens* of the *inaguensis* form: a, habit, × ¼; b, carpellate flower, × 9; c, staminate flower, × 13; d, fruit, × 6; e, seed, × 9; f, infructescence, × 2; g, node showing branches, × 1. Based on *Gillis & Proctor 11575* from Mayaguana Island.

Iresine vermicularis (L.) Moquin in DC. Prodr. **13**(2): 340. 1849.
Lithophila vermicularis (L.) Uline ("-atus"). Field Mus. Publ. Bot. Ser. **2**: 39. 1900.

Philoxerus vermicularis is found throughout the Caribbean. In the Bahamas it is called "sampire" or "salt-weed."

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CYTOLOGY AND EVOLUTION IN HAMAMELIDACEAE [1]

PETER GOLDBLATT AND PETER K. ENDRESS

IN A RECENT REVIEW of cytology in relation to angiosperm phylogeny, Raven (1976) was able to suggest basic chromosome numbers and to formulate hypotheses on the evolution of many major groups. One of the results of the study was to focus attention on phylogenetically critical genera for which cytological data were unknown. With Raven's encouragement and help, material of several genera critical to the understanding of relationships within the Hamamelidaceae *sensu lato*, and of the Hamamelidales as a whole, were sought for cytological study. These genera included *Disanthus, Rhodoleia, Exbucklandia*, and *Altingia*. The first three each represent the sole genus in subfamilies of Hamamelidaceae (Disanthoideae, Rhodoleioideae, and Exbucklandioideae, respectively); *Altingia* with *Liquidambar* comprise the Liquidambaroideae. These four subfamilies, together with Hamamelidoideae, comprise the Hamamelidaceae (*sensu* Harms, 1930). Up to the time the study was undertaken, $x = 12$ had consistently been reported in all seven of the 22 genera of Hamamelidoideae which are known cytologically (TABLE 1), while *Liquidambar* with $n = 16$ (Santamour, 1972) and *Exbucklandia* with $n = 32$ (Mehra & Khosla, 1969) stood out in sharp contrast.

MATERIALS AND METHODS

Diploid counts were made from germinating seedlings of *Rhodoleia teysmannii* and *Altingia excelsa*, material of both having been obtained with the help of Dr. Willem Meijer from Tjibodas Mountain Gardens, Bogor, Indonesia. Root tips for these counts were pretreated in 0.02% aqueous colchicine or 0.003M hydroxy-quinoline for five hours, and were then fixed in 3:1 absolute ethanol: glacial acetic acid. Squashes were made as described by Goldblatt (1976). Counts for *Disanthus cercidifolius* were made from meiotic material, with pollen mother cells being squashed in the usual way and stained in acetocarmine.

RESULTS

Disanthus cercidifolius Maxim., $n = 8$. Material cultivated in Zurich, Switzerland, origin not known, *Endress 3528 (z)*.

Altingia excelsa Noronha, $2n = 32$. Indonesia, Java, Tjibodas Mountain Gardens, Bogor, *Meijer s.n.* (no voucher, representative material at BO).

[1] Mitteilungen aus dem Botanischen Museum der Universität Zürich Nr. 286.

TABLE 1. **Chromosome numbers in Hamamelidaceae.**

SPECIES	HAPLOID NUMBER (*n*)	REFERENCE
HAMAMELIDOIDEAE		
Corylopsis glabrescens Franch. & Sav.	24	Santamour 1965
C. himalayana Griff.	12	Mehra & Khosla 1969
C. pauciflora Sieb. & Zucc.	12	Anderson & Sax 1935, Santamour 1965
C. platypetala Rehd. & Wils.	12	Santamour 1965
C. sinensis Hemsl.	12	Santamour 1965
C. spicata Sieb. & Zucc.	36	Anderson & Sax 1935, Santamour 1965
C. veitchiana Bean	36	Anderson & Sax 1935, Santamour 1965
C. willmottiae Rehd. & Wils.	24	Santamour 1965
Distylium racemosum Sieb. & Zucc.	12	Sugiura 1936
Fothergilla gardenii Murray	36	Ernst 1963
	24 [2]	Weaver 1969
F. major (Sims) Lodd. (incl. *F. monticola*)	24 [2]/36	Anderson & Sax 1935
	24 [2]/36	Ernst 1963
	36	Weaver 1969
Hamamelis vernalis Sargent	12	Anderson & Sax 1935
	12	Ernst 1963
H. virginiana L.	12	Ernst 1963
Parrotia persica C. A. Mey.	12	Pizzolongo 1958
Parrotiopsis jacquemontiana Rehd.	12	Anderson & Sax 1935
Sinowilsonia henryi Hemsl.	12	Anderson & Sax 1935
RHODOLEIOIDEAE		
Rhodoleia teysmannii Miq.	12	present work
DISANTHOIDEAE		
Disanthus cercidifolius Maxim.	8	present work
EXBUCKLANDIOIDEAE		
Exbucklandia populnea R. Br. ex Griff.	32	Mehra & Khosla 1969
LIQUIDAMBAROIDEAE		
Liquidambar orientalis Mill.	16	Pizzolongo 1958, Ernst 1963
L. styraciflua L.	15	Anderson & Sax 1935
	16	Pizzolongo 1958
	15, 16	Ernst 1963
L. styraciflua × *L. orientalis*	16	Santamour 1972
L. styraciflua × *L. formosana* Hance	16	Santamour 1972
Altingia excelsa Noronha	16	present work

[2] According to Weaver (1969), differing numbers in earlier counts were due to misidentification of the specimen.

Rhodoleia teysmannii Miq., $2n = 24$. Indonesia, Java, Tjibodas Mountain Gardens, Bogor, *Meijer s.n.* (no voucher, representative material at BO).

DISCUSSION

The results of this study stress the fundamental divergence within the Hamamelidaceae, with $n = 12$ basic in Hamamelidoideae and now re-

ported in Rhodoleioideae, and $n = 8$, 16, and 32 found to be basic not only in Liquidambaroideae and Exbucklandioideae, but now also in Disanthoideae. Similarities in morphology among genera in these two divergent lines are thus likely to be of considerable taxonomic significance. Several characters are typical, although not strictly exclusive, for one group or the other. For example, pinnate leaf venation, stellate hairs, and one (rarely to three) ovules per carpel (except *Rhodoleia*) are found in the $x = 12$ group, while rather palmate leaf venation, lack of stellate hairs (except *Chunia*), and six or more ovules per carpel occur in the $x = 8$ group.

A second very striking result was the discovery of $n = 8$ in *Disanthus*, making this the first diploid in the otherwise polyploid Hamamelidaceae, and in fact the first diploid in Hamamelidales as circumscribed by Cronquist (1968) and Thorne (1974). This strongly supports the ancestral position within Hamamelidaceae usually assigned to Disanthoideae in phylogenetic treatments.

The flower of *Disanthus* shows a unique combination of characters regarded as primitive in the family: bisexuality, pentamery, double perianth, superior ovary, and the presence of several ovules per carpel. On the basis of leaf morphology, Wolfe (1974) comments that of all Hamamelidaceae he examined, *Disanthus* has foliage most similar to other putatively primitive members of its subclass. Furthermore, it forms a link with the $x = 12$ group, especially with *Hamamelis* and its allies, in inflorescence and flower structure.

The occurrence of a primitive, ancestrally diploid member of Hamamelidaceae makes it probable that the family is not, as previously believed, of polyploid origin. Whether the Hamamelidaceae are regarded in the broad sense, including the Liquidambaroid-Exbucklandioid-Disanthoid line with $x = 8$, or in a more restricted sense, including only the $x = 12$ line, it is clear that the two groups are fundamentally allied, and are derived from a common ancestral stock. Most likely, $x = 7$ is basic in the family, with early aneuploid decrease to $x = 6$ and subsequent polyploidy to give rise to the Hamamelidoid-Rhodoleioid alliance, and aneuploid increase to $x = 8$, still found in Disanthoideae, with subsequent later polyploidy leading to the Exbucklandioid-Liquidambaroid alliance. It is also possible that either $x = 8$ or $x = 6$ is basic, with an aneuploid decrease or increase, respectively.

Significantly, the only other diploids in the Hamamelidiflorae (*sensu* Thorne, 1974), i.e., Casuarinaceae (Casuarinales), Fagaceae, and Betulaceae (Fagales), are *Casuarina* ($x = 8$, 9 with 8 in the more primitive members of the genus) and *Carpinus*, *Ostrya*, and *Ostryopsis* (all $x = 8$) of the Betulaceae-Coryloideae. The occurrence of similar base numbers in Hamamelidaceae and Casuarinaceae is of particular importance since it now makes a relationship between these two plausible on cytological grounds, where previously the low base number in the very specialized Casuarinaceae seemed inconsistent with such a hypothesis.

Endress (1967) has shown that the Betulaceae are indeed very closely

related to the Hamamelidaceae, and that the two families have a large number of common characters, especially in the areas of floral structure and development. It is interesting to note that the Coryloideae (except *Corylus*) with the closest affinity to the Hamamelidaceae, have the same basic chromosome number, $x = 8$, whereas the other genera of the family with $n = 14$ could possibly be derived from $x = 7$. On the other hand, on morphological grounds, the Betulaceae appear more closely related to the $x = 12$ group of the Hamamelidaceae than to living members of the $x = 8$ group, so that if Hamamelidaceae and Betulaceae are as closely related as suggested here, the lines leading to these families must have diverged before polyploidy became established in either one.

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COVER: The conelike follicetum or fruit aggregate of *Magnolia tripetala* L., an American species of section Rhytidospermum Spach, is the basis for our new cover design. Individual follicles of the fruiting body were used in the devices for other parts of the Journal and for the offprints. The designs were all drawn by Karen S. Velmure, who also planned and prepared the three preceding covers for the Journal, as well as the accompanying devices.

The section Rhytidospermum, of which *Magnolia tripetala* is the type, includes three species of Asia and four to six of America. These are large shrubs or deciduous trees with leaves crowded into false whorls at the end of branchlets, alternate and widely spaced on new shoots. *Magnolia tripetala*, the umbrella-tree or elkwood, is native in rich woods of eastern North America from southern Pennsylvania and West Virginia, south into Florida, and westward through Ohio and Kentucky to Arkansas and Missouri. It is sometimes found escaped from cultivation north into central Massachusetts. In cultivation it has been involved in many hybrid combinations.

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SYSTEMATICS OF THE NEOTROPICAL GENUS CENTRADENIA (MELASTOMATACEAE)

FRANK ALMEDA, JR.

CENTRADENIA IS A WELL-DEFINED GENUS of subshrubs and suffrutescent perennial herbs comprising six taxa which are largely restricted to Mexico and Central America. The genus is unique among Mesoamerican Melastomataceae in having basally oblique leaves; pyriform, clavate, or dolabriform seeds with a conspicuous lateral raphe; and pronounced anisophylly. Despite its small size, comparatively limited range, and remarkable diversity in androecial morphology, *Centradenia* has never been the subject of a comprehensive study. Because previous knowledge of the genus has been limited to regional floristic surveys, the limits and ranks of certain taxa have remained controversial. This study was undertaken in an effort to clarify the confusion by providing new information on chromosome numbers, ecogeographic distribution patterns, and the breeding systems of selected taxa. Based on the cumulative information obtained from these approaches together with an evaluation of morphological criteria, I here recognize four species (two of which are divided into two subspecies).

TRIBAL AND GENERIC CONSIDERATIONS

The genus *Centradenia* has been assigned by various authors to two of the five neotropical tribes of Melastomataceae with capsular fruits, the Tibouchineae (Krasser, 1893) and the Microlicieae (Cogniaux, 1891; Hooker, 1867; Triana, 1871). Tribal disposition of genera in the family has rested heavily on characters such as capsule symmetry, position of staminal appendages, prolongation of the connective, and seed shape. Krasser apparently emphasized the ventral position of appendages when he relegated *Centradenia* to the Tibouchineae; Cogniaux, Hooker, and Triana, however, gave greater weight to seed shape when they assigned it to the Microlicieae.

Tribal limits, especially among the Microlicieae, Rhexieae, and Tibouchineae, are not always clear. Consequently, tribal assignment often depends in large part upon which of the differences and similarities in stamens and seeds one chooses to emphasize. In a family such as the Melastomata-

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ceae, where floral evolution has been extensive. one may logically conclude that the diverse floral types represent adaptations to different pollination systems. Therefore, caution must be used in any infrafamilial classification emphasizing floral features that appear to be evolutionarily labile. A focus on seemingly conservative characters such as the shape and surface patterning of seeds may provide a better approximation of affinities. This view is supported by the recent SEM study by Whiffin and Tomb (1972) of seed morphology in neotropical capsular-fruited Melastomataceae. Although their study essentially confirms the existence of five capsular-fruited tribes in the New World (see TABLE 1). it brings into question the delimitation of certain groupings as well as the disposition of selected genera. For example, the variously sculptured clavate or pyriform seeds of *Centradenia* have a conspicuous lateral raphe which is reminiscent of a modified bertolonioid seed but clearly unlike anything considered typical of the Microlicieae or Tibouchineae. Although current placement of *Centradenia* in the Microlicieae is, therefore, questionable, on the basis of present evidence I reject the expedients of tribal transfer or establishment of a new tribe to accommodate it.

A search for the closest generic relatives of *Centradenia* has contributed little to a clarification of its systematic position. *Centradenia* does not appear to be closely allied to any of the predominantly South American genera with which it was associated in the most recent familial monograph by Cogniaux (1891), or to have any close relatives among other Melastomataceae in Mexico and Central America. In describing *Centradeniastrum*, a poorly known ditypic genus of Colombia and Peru, Cogniaux (1908) placed it close to *Centradenia* in the Microlicieae, but he neglected to comment on the characters used to ascertain this relationship. Macbride (1941) also emphasized a close alliance between these two genera, but his suggestion to combine them seems unwarranted in view of their striking differences in vegetative, floral, and fruit characters. As with *Centradenia*, seed morphology of *Centradeniastrum* differs markedly from that of typical Microlicieae. The seeds of *Centradeniastrum album* Gleason are basically clavate with an asperulate testa; the broad expansion of the raphe into a flat wing on all sides of the embryo imparts a conspicuous pyramidate outline.

Although my study has not been sufficiently extensive to establish new tribal or generic limits, it seems evident that realignments will be needed as additional data become available. Based on present information, the seeds of *Centradenia* and *Centradeniastrum* are probably best interpreted as divergent modifications based on the bertolonioid theme. The relationships of these genera to each other or to members of the Bertolonieae is unclear and cannot be evaluated with confidence until other neotropical genera in the family are studied.

COMPARATIVE MORPHOLOGY

The following paragraphs provide a brief conspectus of the morphological features judged to be of taxonomic value in *Centradenia*. Herbarium

TABLE 1. **Differences among the Neotropical Capsular-fruited Tribes of Melastomataceae.**†

	CAPSULE SYMMETRY	STAMINAL APPENDAGE	CONNECTIVE PROLONGED BELOW THECAE	SEED SHAPE	SEED SURFACE PATTERN
MICROLICIEAE	terete or angulate	ventral	usually	oblong to cochleate	foveolate
TIBOUCHINEAE	terete or angulate	ventral	usually	cochleate	tuberculate
RHEXIEAE	terete	dorsal *	rarely **	cochleate	tuberculate, rugose, or costate
MERIANIEAE	terete or angulate	dorsal	rarely	cuneate or fusiform (often winged)	smooth, lightly foveolate, or minutely asperulate
BERTOLONIEAE	3–5-angled or -winged	ventral or dorsal	usually	cuneate, clavate, or pyramidate	tubercular-papillate to asperulate with a lateral raphe along the length of the seed

† Modified after Cogniaux (1891) and Whiffin & Tomb (1972).
* The stamens of *Pachyloma* have both dorsal and ventral appendages.
** *Pachyloma* invariably has prolonged connectives.

and fluid-preserved specimens have formed the basis for these descriptive notes, but most conclusions on variability are tempered by field observations and analysis of specimens prepared from cultivated material.

HABIT AND DURATION. All species of *Centradenia* have been described as suffrutescent herbs or well-developed shrubs; a few have even been reported as annuals on herbarium labels. Genetically, *C. paradoxa* and *C. grandifolia* are capable of attaining shrubby dimensions of 1 to 2 meters under optimal conditions in the field, but most individuals of the species that I have seen are best described as soft-woody subshrubs or suffrutescent perennial herbs with root systems that are fibrous and much-branched. Riedel (1957) notes that *C. grandifolia* and *C. floribunda* become as tall as 2 feet in cultivation, whereas *C. inaequilateralis* is generally smaller. All of these taxa are reportedly short-lived in cultivation, and *C. inaequilateralis* has been observed to behave as an annual under greenhouse conditions (Don, 1832; Wurdack, pers. comm.). This may suggest that these species are facultative annuals or biennials, with some individuals dying after one or two years of growth and others becoming established as perennials.

STEMS AND BRANCHING. The stems of *Centradenia grandifolia* are unique in being stout, conspicuously quadrangular, and typically winged at the junction of adjacent faces. In all other species the stems are slender and terete or subquadrangular, with one pair of narrow, flat to concave faces and a wider pair of rounded to convex faces. The branches of all species are alternate, more or less laxly disposed, and horizontally spreading from a central axis or strict to ascending with primary branches initiated in sympodial fashion from or near ground level.

LEAVES. Leaf arrangement in *Centradenia* is opposite and decussate, but the leaves on arching branches of *C. inaequilateralis* often assume a distichous orientation brought about by a twisting of the petioles. All species are characterized by a pronounced size dimorphism of paired leaves (anisophylly) such that the larger leaves alternate from one side of the stem to the other at each successive node. In *C. grandifolia*, *C. inaequilateralis*, and *C. paradoxa*, the smaller prevailingly sessile leaf is frequently early deciduous, conveying a false impression of alternate phyllotaxy. Judging from its constancy in cultivated material, anisophylly in *Centradenia* undoubtedly has a genetic basis and is therefore of taxonomic value in characterizing the genus. Less is known about the functional significance of this peculiar foliar arrangement. Since *Centradenia* often inhabits sheltered or shaded habitats along forest streams or waterfalls, anisophylly may provide optimal accommodation of large and small leaves with minimal overlap, thereby enhancing light reception and increasing photosynthetic efficiency. If this speculation is correct, it would parallel the situation recently described for certain terrestrial anisophyllous species of *Columnea* (Gesneriaceae) by Morley (1973, 1974). Blades of the larger leaves are petiolate, plinerved, broadly to narrowly lanceolate, and generally asym-

metric at the base. Leaves with symmetric and asymmetric bases are not infrequently found on the same plant in such species as *Centradenia floribunda* and *C. inaequilateralis*. There are modal interspecific differences in leaf size, ranging from the smallest in *C. inaequilateralis* to the largest in *C. grandifolia*, but the susceptibility of this character to environmental modification makes it unreliable for a strict delineation of taxa.

PUBESCENCE. Three basic types of epidermal appendages may be recognized: smooth, unbranched, multicellular trichomes; glandular trichomes with multicellular stalks terminated by a globose cell; and appressed, translucent bacilliform structures that are actually clavate and multicellular when viewed under a light microscope. The latter, which measure about .25 mm. in length, are restricted to the young hypanthia and upper foliar surfaces of *C. inaequilateralis*. The presence, absence, and relative abundance of pubescence on stems, leaves, floral bracts, hypanthia, and petals vary considerably among individuals or populations. When a vestiture is present, multicellular trichomes predominate, but these are frequently associated with glandular hairs on peduncles of the inflorescence, floral bracts, hypanthia, and petal margins of most species. The length and posture of cauline trichomes are sufficiently variable to preclude taxonomic utility. In contrast, the length and attitude of hypanthial trichomes in *C. floribunda* and *C. inaequilateralis* are constant and diagnostic.

INFLORESCENCES. *Centradenia* is rather unique for a small genus in having both determinate and indeterminate inflorescences. Earlier workers (Gleason, 1958; Standley, 1938; Standley & Williams, 1963) described the inflorescence as solitary, few-flowered, or cymose. Although these descriptions are basically correct, a reappraisal of floral arrangements reveals greater diversity in both structural and developmental attributes than was previously thought.

The inflorescence of all taxa is derivable from the basic compound dichasial pattern characteristic of *C. grandifolia*. Borne in terminal and axillary positions, the dichasia vary greatly in size, compactness, and number of flowers. The branching pattern, like that of foliar arrangement, is opposite and decussate, with the primary axis producing a succession of nodes and subsidiary branches which terminate in simple dichasia. In decompound structures with basal branches that are longer than those emanating from successive nodes, the inflorescence is commonly corymbiform in outline. The seemingly endless variations on the dichasial scheme are generated by amplification of the structural units already described, or by one or more of the following modifications:

1.) Reduction in length of primary and secondary axes.
2.) Terminal bud abortion of primary and/or secondary axes.
3.) Irregular abortion of floral buds.
4.) Complete suppression of secondary and/or tertiary branching.

The combined effects of the first three modifications listed above produce the inflorescence type typically encountered in *C. paradoxa*. It is gen-

erally diffuse and irregularly branched, and often consists of single flowers, paired flowers, and simple dichasia, collectively. At times, the degree of reduction is such that the inflorescence is superficially racemose, but differs in having basipetal rather than acropetal floral maturation.

The most significant modification of the compound dichasium is seen in *C. floribunda*, which exhibits a sparingly branched panicle consisting of two to six racemes diverging from common or proximal nodes at the base of the inflorescence. This structure is apparently derived by abortion of the primary axis and suppression of tertiary branching coupled with a shift from basipetal to acropetal floral maturation. Extreme reductions of an indeterminate structure such as the sparsely branched panicle often result in the short, solitary racemes so characteristic of *C. inaequilateralis*. Racemes may, in turn, be further modified by reduction of the central axis and abortion of floral buds to produce subfasciculate clusters and solitary flowers, respectively.

Despite their structure and developmental sequence, floriferous branches are always delimited by highly modified leaves (floral bracts) which subtend nodes and floral pedicels. These are thinly membranaceous or scale-like and rather inconspicuous. They differ sufficiently in form and vestiture to be of value in specific distinctions, but in most species they are caducous and are preserved only infrequently in herbarium material.

HYPANTHIUM AND CALYX. Mature hypanthia exhibit a series of subtle but diagnostic variations. They are terete or angulate, and range in shape from subcylindric through campanulate to urceolate or globose. Vasculation consists of eight ± evenly spaced longitudinal ribs crowned by a circular ring conventionally called the torus. The four calyx lobes extending from the torus are broadly deltoid to truncate and are usually erect at anthesis and on fruiting hypanthia. The unusual hypanthia of *C. grandifolia* subsp. *grandifolia*, accrescent and somewhat bladdery, loosely envelop the ovary at maturity.

PETALS. Each of the four petals is inserted at a point on the torus opposing a stamen and alternating with a calyx lobe. The petals are dextrorsely convolute in bud and oriented in a horizontal plane or campanulate conformation when fully expanded. Although most petal characters are insignificant for specific delimitation, variations in size and color are useful in characterizing certain taxa. Petals of all species are broadly to narrowly obovate, entire to obscurely crenulate, and glabrous except for the margins which are sometimes fringed with smooth or glandular trichomes.

ANDROECIUM. The androecium of all species consists of eight poricidal stamens. In each species the stamens are differentiated into one of three size classes, ranging from strongly dimorphic through weakly dimorphic to subequal. Filament insertion on the torus is identical to that typically found in other genera of the family. The four stamens of the larger whorl

oppose the sepals and alternate with the four stamens of the smaller whorl which oppose the petals. In bud, filaments of all stamens are bent inward and downward, so that the ventral sides of the thecae face the interior surface of the hypanthial wall. The anthers of both whorls are smooth to undulate, 2-celled, and ventrally channeled. The connective is variously prolonged below the thecae and modified ventrally at the point of filament insertion into upturned or deflexed appendages of varying morphology. Connective length, and the size, shape, and color of anthers and appendages, provide valuable taxonomic criteria and undoubtedly have significance in the chain of events leading to pollination.

In expanded flowers the posture and spatial relationship of the style and stamens conform to one of two basic patterns. In *C. floribunda* subsp. *floribunda* and *C. paradoxa*, which have weakly dimorphic and subequal stamens, respectively, the anthers are connivent or slightly spreading around the more or less straight style, so that the stigma is situated among the anthers. In *C. paradoxa* the style often extends somewhat beyond the poricidal anthers.

In the second pattern the stamens are conspicuously dimorphic, and the style is permanently declined to one side of the flower. Filaments of the smaller staminal whorl are erect but somewhat twisted, so that the ventral surfaces of the thecae face away from the central axis of the flower. Filaments of the larger whorl may be erect or declined to that side of the flower occupied by the style. In either case, the geniculate bend in the stamens at the junction of filament and connective brings the anthers into a subparallel orientation more or less removed from the stigma. This complex androecial conformation recalls the pattern typically found in *Heterocentron*, a species of which is accurately illustrated by Ziegler (1925, *fig. 70*).

In general, declinate styles and strongly dimorphic stamens are correlated with prolonged connectives and elaborate appendages, whereas straight styles and connivent stamens correlate with reduction in length and complexity of these structures. The floral differences exhibited by these two groupings are basically the ones used by Cogniaux (1891) when he chose to divide the genus into two sections. Continued recognition of Cogniaux's infrageneric classification is untenable since it would demand the segregation into separate sections of the subspecies of *C. floribunda* recognized here. Furthermore, it would necessitate inclusion of *C. floribunda* subsp. *floribunda* and *C. paradoxa* in the same section. The similar floral features of these two taxa apparently represent convergent modifications which presumably enhance the probability of self-pollination. In this respect it is important to emphasize that they are more similar to outcrossing species with dimorphic stamens and declinate styles than they are to each other.

GYNOECIUM AND FRUIT. The essentially glabrous, 4-locular ovary is superior but fully enveloped by the hypanthium throughout its development. The apical portion of the ovarial wall may be glandular-ciliate as

in *C. paradoxa*, or variously elaborated distally into setose or ciliate outgrowths surrounding the stylar scar. The linear, glabrous style terminates in a punctiform stigma and assumes a stabilized posture ranging from more or less straight to declinate.

The fertilized gynoecium develops into a dry, thin-walled loculicidal capsule with axile placentation and usually persists on the infructescence long after all seeds have been dispelled.

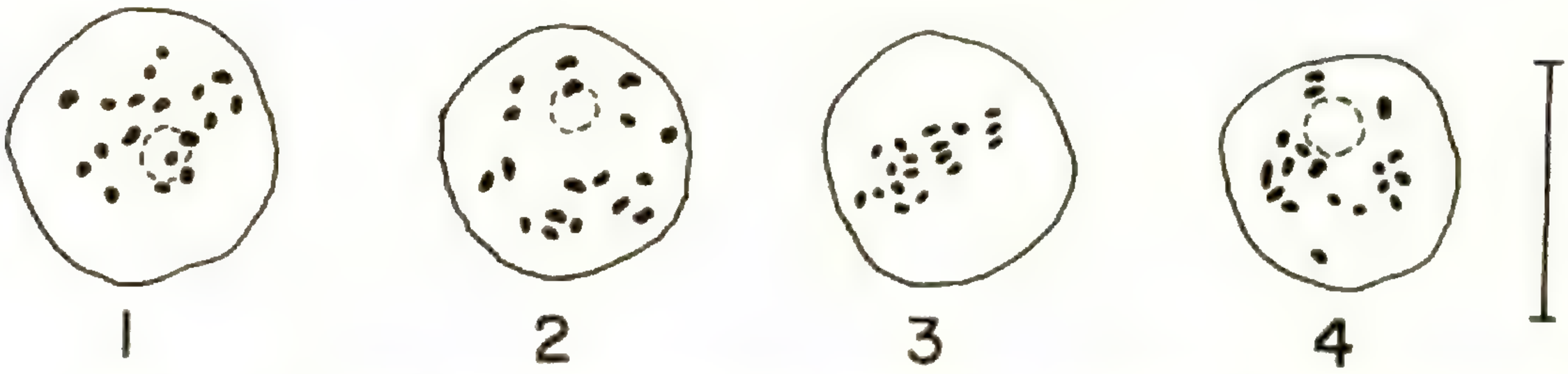
SEEDS. The seeds, which show little variation in size (0.5–1.0 mm. long), range in shape from narrowly pyriform to clavate or dolabriform, and consistently exhibit a longitudinal raphe extending along the length of the seed. Surface patterning ranges from papillate through muriculate or verrucose to echinate. The conservatism of seed characters in the family makes the diversity in *Centradenia* particularly valuable for drawing specific distinctions.

CYTOLOGY

Chromosome number determinations were made from diakinesis or metaphase I configurations in microsporocytes. Flower buds were fixed in the field for at least 24 hours in acetic ethanol (1:3), washed, and subsequently stored in 70 percent ethanol under refrigeration. The contents of immature anthers were squashed in acetocarmine. Voucher specimens for chromosome number determinations listed in TABLE 2 are deposited

TABLE 2. **Chromosome Numbers in Centradenia.**

TAXON	HAPLOID NUMBER	COLLECTION DATA
C. floribunda subsp. **floribunda**	$n = 18$	Cultivated: Longwood Garden (accession no. 631027), *Wurdack 2546*
C. grandifolia subsp. **grandifolia**	$n = 18$	Costa Rica. San José: 27 km. SE of Cartago, *Almeda 2677*
	$n = 18$	Costa Rica. San José: 9 km. N of San Isidro, *Almeda 2701*
	$n = 18$	Costa Rica. San José: 20–28 km. N of San Isidro, *Almeda 2704*
C. inaequilateralis	$n = 18$	Costa Rica. San José: 3–6 km. N of Las Nubes, *Almeda 2629*
	$n = 18$	Costa Rica. Alajuela/Heredia border: Varablanca, *Almeda 2652*
C. paradoxa	$n = 18$	Costa Rica. San José: 16–24 km. S of San Isidro, *Almeda 2692, 2693*



FIGURES 1–4. Camera lucida drawings of meiotic chromosome configurations in *Centradenia*. Scale line equals 12 micrometers (μm.). 1 & 2, *Centradenia paradoxa*, $n = 18$, diakinesis; 3, *Centradenia inaequilateralis*, $n = 18$, metaphase I; 4, *Centradenia grandifolia* subsp. *grandifolia*, $n = 18$, diakinesis.

in the herbarium of the University of California, Los Angeles (LA) and/or the United States National Herbarium (US).

The haploid chromosome number for all taxa examined is 18 with normal meiosis (FIGURES 1–4). These counts are the first reports for *Centradenia grandifolia*, *C. inaequilateralis*, and *C. paradoxa*. The only previous chromosome count in *Centradenia* was published by Heitz (1926), who reported $2n =$ ca. 24 for *C. floribunda*. Since that count was made from sectioned material, it may be erroneous and should be disregarded until reconfirmed. Unfortunately, Heitz cited no voucher specimens, so the identity of the plant he examined cannot be verified. The unpublished count of $n = 18$ for *C. floribunda* subsp. *floribunda*, which is reported here through the courtesy of J. J. Wurdack and M. L. Solt, casts further doubt on the number provided by Heitz and suggests that *Centradenia* may be homogeneous cytologically. Meaningful comparisons with other genera in the Microlicieae or Bertolonieae are not yet possible because of the paucity of published chromosome numbers for neotropical Melastomataceae. The only reliable published counts for members of these tribes are those of Davidse (1970), who reported a count of $n = 20$ for *Rhynchanthera paludicola* (J. D. Smith) Gleason and Sugiura (1940), who reported $n = 14$ for *Bertolonia maculata* DC. A haploid number of 18, however, is a relatively high basic number among angiosperms (Grant, 1971; Stebbins, 1971) and may indicate a polyploid origin for *Centradenia*.

BREEDING SYSTEMS

Information on the breeding system in *Centradenia* is limited to that derived from preliminary experimental manipulations of *C. grandifolia* subsp. *grandifolia* and *C. paradoxa* conducted under field conditions in Costa Rica. Following the procedures outlined elsewhere (Almeda, 1975), self-pollinations and complete staminal emasculations were performed on flowers of several individuals. In addition, a number of flowers were tagged and left open to potential pollinators in order to provide a comparative estimate of fruit set between open and artificially pollinated flowers. The primary objective of these exclosure experiments was to test for self-compatibility and apomixis. All emasculated, unpollinated flowers

TABLE 3. **Summary of Artificial and Controlled Pollinations of Selected Centradenia Species.**

SPECIES	NUMBER OF INDIVIDUALS TESTED	NO. OF FLOWERS TESTED			NO. OF FLOWERS SETTING FRUIT		
		OPEN POLLINATION	SELF POLLINATION	STAMINAL EMASCULATION	OPEN POLLINATION	SELF POLLINATION	STAMINAL EMASCULATION
C. grandifolia	14	42	40	32	40	2	0
C. paradoxa	10	30	43	20	29	39	0

of both species aborted approximately one week after peak stigmatic receptivity (see TABLE 3). This suggests that apomixis is not employed as a reproductive mechanism by these taxa. The results of artificial self-pollinations indicate that a strong incompatibility system is present in *C. grandifolia* but not in *C. paradoxa*, since the latter sets plump capsules with fully formed seeds comparable in all respects to controlled open-pollinated flowers. The structural and spatial attributes of floral parts in *C. grandifolia* and *C. paradoxa* are therefore significant since they act to promote outcrossing and inbreeding, respectively.

As noted under the discussion of morphology, the flowers of *Centradenia* species can be grouped into two categories according to the posture and spatial orientation of the style and stamens in relation to one another. Flowers of the outcrossing *C. grandifolia* have brightly colored petals ranging through various hues of pink. Upon floral expansion under mid-morning sunshine, the style becomes displaced to one side of the flower and assumes an abrupt apical curvature so that the stigma faces the central axis of the flower. The eight stamens comprising the androecium are dimorphic and are differentiated into two distinct whorls. The antepetalous stamens are comparatively small, yellow in color, and more or less erect at anthesis. The larger, magenta anthers of the antesepalous whorl are characterized by a geniculate bend at the point of filament insertion, which brings the anthers into a subparallel, platformlike conformation with apical pores extending well above or beyond the opposing stigma. The orientation of floral parts is such that the yellow appendages of the larger anthers are situated among the smaller, erect anthers. Hence, any disturbance of the small anthers elicits a concomitant movement of the larger anthers via the appendages. The spatial relationship of floral parts remains unchanged during the three to four day life of a flower. The poricidal nature of the anthers, together with their physical separation from the stigma, therefore suggests a system highly dependent on biotic manipulation for effective pollination. The flowers of *C. grandifolia* produce no detectable odor or nectar, but a visual signal consisting of the smaller yellow anthers and associated appendages apparently plays a key role in attracting pollen-seeking bees to the flower. I have observed bees of the genera *Bombus*, *Melipona*, and *Trigona* visiting the flowers of *C. grandifolia*. *Bombus* and *Melipona* always approach a flower facing the erect yellow anthers and then proceed systematically to probe each of them for pollen. *Trigona* is erratic and especially destructive in its pollen-foraging activities and often perforates or severs the larger anthers during its routine search for pollen among the smaller anthers. Because of their visitation method and small size, *Melipona* and *Trigona* rarely make physical contact with the stigma and are probably inconsequential as pollinators. In contrast, flower visitation by *Bombus*, the most frequent insect visitor noted in the course of my observations, is similar to the effective buzz pollination mechanism previously described for other Melastomataceae (Almeda, 1975; van der Pijl, 1939). Upon alighting on the landing platform of the flower provided by the larger subparallel stamens,

Bombus makes ample contact with the stigma, stamens, and appendages. Pollen discharge from the poricidal anthers is effected by a vigorous vibratory movement of the bee's thorax, accompanied by little or no perceptible wing movement. Therefore, the dimorphic androecium of *C. grandifolia*, like that of other Melastomataceae (Harris, 1905; Proctor & Yeo, 1973), has two important functions: the smaller, erect anthers provide pollen as an attractant, while the larger, geniculate anthers function in pollination. Although varying degrees of pollen viability have been reported for one or both sets of anthers in *Melastoma malabathricum* L. (Percival, 1965) and other angiosperm phylads with similar pollen presentation mechanisms (Bowers, 1975; Buchmann, 1974), I have found no significant reduction in pollen viability between the two types of anthers in any one flower of *C. grandifolia*.

Centradenia paradoxa exhibits the opposite extreme in floral morphology. The petals are invariably white and expand to a campanulate or bowl-like conformation. The yellow, subequal anthers have greatly reduced connectives and appendages and form a closely connivent cone around the straight style, which extends somewhat beyond the apex of the anthers. These features, in concert with the nodding posture of the flowers and the homogamous maturation of floral organs, appear to foster self-pollination. The jarring forces of wind and rain may also play a role in selfing, but the amount of autogamous reproduction in natural populations cannot be stated categorically at this time.

The natural pollinators of *Centradenia paradoxa* have not been seen during field studies. In *Dodecatheon* (Primulaceae), *Solanum* and *Lycopersicon* (Solanaceae) (all of which have flowers that are morphologically very similar to *C. paradoxa*), Macior (1964) has demonstrated that pollination is accomplished by bees which, while hanging in an inverted position, sift pollen from the pendent anther cone by rapid vibrations. Insect-mediated pollination of *C. paradoxa* is probably effected in a similar manner. The abundance and flight pattern of pollen vectors and the number of flowers per individual or inflorescence will, however, impose regulating influences on the relative amounts of geitonogamy (pollen transfer between flowers on the same plant) and xenogamy in natural populations.

Little is known about the reproductive biology of other species in the genus. If the structure and spatial relationship of floral parts can be used to make inferences, I would rank *Centradenia floribunda* subsp. *bernoullii* and *C. grandifolia* subsp. *brevisepala* as outcrossing species. The floral structure of *C. inaequilateralis* is reminiscent of an outcrosser, but the comparatively small flowers seem to close at dusk and during inclement weather, opening under the influence of bright light or sunshine. The effects of opening and closing movements on intrafloral pollen dispersion are unknown. Faegri and van der Pijl (1971) suggest that floral closing movements may serve as an effective pollination mechanism for self-compatible angiosperms. This speculation remains to be demonstrated for a species possessing poricidal anthers.

Centradenia floribunda subsp. *floribunda* is similar to *C. paradoxa* in having a straight style and more or less connivent anthers. The stigma is situated among the anther pores, but the flowers are held in erect fashion and apparently lack a mechanism to insure self-pollination in the absence of mechanical disturbance. According to Darwin (1876), *C. floribunda* sets abundant seed when artificially pollinated, but seed set is sporadic and unpredictable when plants are screened from potential pollinators.

Geography and Ecology

The distribution of *Centradenia* extends from Hidalgo, Mexico, southeastward through Central America to Panama, with one species known from outlying stations in the Chocó lowlands on the Pacific coast of Colombia. This range parallels that of the monotypic genus *Schwackaea*, and to a lesser extent that of *Heterocentron*, which is centered in Mexico and northern Central America. These distribution patterns are noteworthy because almost all other neotropical genera in the family with species in Mexico and Central America have centers of diversity in South America.

The elevational amplitude for several taxa in *Centradenia* appears to be between 200 and 1900 meters, although *C. paradoxa* is presently unknown from elevations above 1200 meters, and *C. grandifolia* occurs primarily at elevations between 1300 and 2500 meters. All species are restricted in habitat, occurring most commonly on sheltered roadbanks, margins of streams and disturbed forests, or moist cliffs in the spray of waterfalls. *Centradenia floribunda* and *C. inaequilateralis* frequently maintain a foothold in the shallow soil accumulation of fissured boulders in or along streams. Field experience with three of the species leads me to suspect that partial shade and high moisture are requirements for their optimal development. Since wet, sheltered habitats are in themselves discontinuous elements of the landscape even in the tropics, the disjunct and sharply delimited population structure of each species is understandable. Large, inexplicable distributional gaps remain, however, for the comparatively wide-ranging species such as *C. grandifolia* and *C. inaequilateralis*. The typical subspecies of *C. grandifolia*, for example, occurs in eastern Mexico, western Guatemala, Honduras, and Costa Rica, but apparently is absent from what appear to be suitable habitats in Honduras, El Salvador, and Nicaragua.

Although the ranges of two or more species overlap in southeastern Mexico, western Guatemala, Honduras, and Costa Rica, I have been unable to find two species growing together or in closely adjacent populations. Sympatry would not be unusual in view of the similar habitat requirements and the overlapping elevational tolerances of several taxa.

The taxa exhibiting straight styles and connivent anthers have significant distributions in that they geographically replace their closest relatives which have flowers adapted for outcrossing. Thus, the outcrossing *C. floribunda* subsp. *bernoullii* of Honduras and El Salvador is replaced

by the typical subspecies in Guatemala and contiguous Mexico. Similarly, the outcrossing *C. grandifolia* subsp. *grandifolia*, which reaches its southern limit in the highlands of Costa Rica, is replaced both elevationally and geographically by *C. paradoxa* as one moves south and east of the Cordillera de Talamanca.

TAXONOMIC TREATMENT

Centradenia G. Don, Gen. Hist. Dichl. Pl. 2: 765. 1832.

Erect shrub, subshrub, or suffrutescent perennial, with strict and somewhat congested to loosely fastigiate branching from a shallow fibrous root system. Distal cauline internodes glabrous to pubescent, terete, subquadrangular, or markedly quadrangular with carinate or prominently winged stem angles. Leaves opposite, decussate, petiolate, or sessile, strongly dimorphic to subequal in each pair, basically oblique or ± symmetric, lanceolate, glabrate to copiously pubescent, plinerved. Inflorescence terminating main stems and upper lateral branches, basically a multiflowered (sometimes corymbiform) dichasium, but frequently becoming paniculate, racemose, or subfasciculate by reduction; bracts subtending floral pedicels and nodes of the inflorescence sessile, caducous, often thinly membranaceous and translucent. Flowers perigynous; hypanthium free from the ovary but fully enveloping it, urceolate to campanulate, terete or ± quadrangular, 8-nerved, crowned by a circular vascular ring (torus) bearing sepals, petals, and stamens. Sepals persistent, erect to slightly spreading, broadly deltoid to triangular-ovate or truncate. Petals 4, free and spreading or connivent and somewhat cupulate, white or pink to magenta, fugacious, obovate, entire to remotely crenulate. Stamens 8; strongly dimorphic to subequal, composed of 4 larger stamens in an antesepalous whorl and 4 smaller ones in an antepetalous whorl; filaments glabrous, compressed, and ligulate; anthers 2-celled, glabrous, linear-oblong, subulate or elliptic-ovate to obovate, and terminated by a solitary circular pore, connective prolonged below the thecae and variously modified ventrally into sessile or prolonged, upturned, vascularized appendages. Pollen white, prolate-spheroidal, 11.2–17.5 μm. in diameter, the three colporate apertures alternating with three pseudocolpi, sculpturing smooth to obscurely rugulate. Ovary superior, ovoid to obovoid, mostly glabrous but typically pubescent at the summit, quadrilocular with axile placentation; ovules numerous, anatropous, and borne on placental intrusions. Style glabrous, linear, straight or somewhat sigmoid and declinate; stigma punctiform. Capsule dry, semiwoody, loculicidal. Seeds narrowly pyriform to clavate or dolabriform, echinate (often glandularly so), verrucose to muriculate or papillate.

√TYPE SPECIES. *Centradenia inaequilateralis* (Schlechtd. & Cham.) G. Don.

Key to the species and subspecies of Centradenia

A. Inflorescence a short raceme or subfasciculate cluster of (1–)2–4(–6) flowers, axis typically less than 1 cm. long; hypanthia ± quadrangular, sparsely pubescent, the trichomes smooth, antrorsely to widely spreading, and typically 0.5–1.5(–2) mm. long. ..... 1. *C. inaequilateralis.*

A. Inflorescence a multiflowered (often corymbiform) dichasium or a paniculate cluster of 2–6 elongate racemes diverging from one another ± basally, axis typically (4–)6–18 cm. long; hypanthium ± terete, often obscurely ribbed by longitudinal vascular strands, glabrous, glandular-puberulent, or beset with a mixture of antrorsely spreading smooth and glandular pubescence, the trichomes typically less than 0.5 mm. long.

B. Stamens weakly dimorphic to isomorphic, differing primarily in size, otherwise similar in coloration and posture, stamens of the larger (antesepalous) whorl straight and ± connivent around the straight style.

C. Smaller leaf at each node sessile, usually early deciduous; anther thecae subulate, 3–4 mm. long, conspicuously undulate ventrally; connective prolonged basally at point of filament insertion into a dilated, facially flattened, triangular spur or tubercle; seeds clavate, beset with numerous glandular setose processes. Costa Rica, Panama, and Colombia. ..... 2. *C. paradoxa.*

C. Smaller leaf at each node petiolate, usually persistent; anther thecae elliptic-obovate, 1–1.5 mm. long, smooth to weakly channeled ventrally; connective prolonged basally into a ± compressed bilobate or trilobate appendage; seeds narrowly pyriform to clavate, obscurely papillate to muriculate. Mexico and Guatemala. ..... 3a. *C. floribunda* subsp. *floribunda.*

B. Stamens distinctly dimorphic, differing primarily in size, posture, and coloration, stamens of the larger (antesepalous) whorl geniculate, forming a subparallel, platformlike conformation opposing the declinate style.

D. Distal cauline internodes conspicuously quadrangular, strongly carinate or winged; smaller leaf at each node falcate to subulate, sessile or subsessile, often early deciduous; connective of the larger (antesepalous) staminal whorl prolonged ventrally into a dilated, upturned, bluntly bifurcate, clavate appendage. Mexico, Guatemala, and Costa Rica.

E. Hypanthia globose to urceolate, broadest at the middle, accrescent and bladdery at maturity with conspicuous reticulate venation between the longitudinal vascular ribs; sepals ovate, apically rounded; petals pink; seeds clavate, beset with numerous setose processes. ..... 4a. *C. grandifolia* subsp. *grandifolia.*

E. Hypanthia campanulate, broadest distally at the torus. closely enveloping the ovary at maturity and lacking conspicuous reticulate venation between vascular ribs; sepals depressed-ovate, apically rounded, truncate or mucronulate; petals white, seeds clavate to dolabriform, beset with low, domelike processes. ..... 4b. *C. grandifolia* subsp. *brevisepala.*

D. Distal cauline internodes ± terete to inconspicuously quadrangular but not strongly carinate or winged; smaller leaf at each node lanceolate, petiolate, usually persistent; connective of the larger staminal whorl prolonged ventrally into a compressed, upturned, ± obtriangular or

linear-oblong appendage bearing two terminal caudiform processes. El Salvador and Honduras. ..... 3b. *C. floribunda* subsp. *bernoullii*.

1. **Centradenia inaequilateralis** (Schlechtd. & Cham.) G. Don, Gen. Hist. Dichl. Pl. 2: 765. 1832. FIGURE 5.

Rhexia inaequilateralis Schlectd. & Cham. Linnaea **5**: 567. 1830. TYPE: Mexico. Veracruz: Cuesta Grande de Chiconquiaco, *Schiede & Deppe 565* (holotype: presumably at B and destroyed during World War II; isotype: US!).

Rhexia parvifolia Schlechtd. Linnaea **13**: 428. 1839. *nomen illegit.*, Art. 63. I.C.B.N.

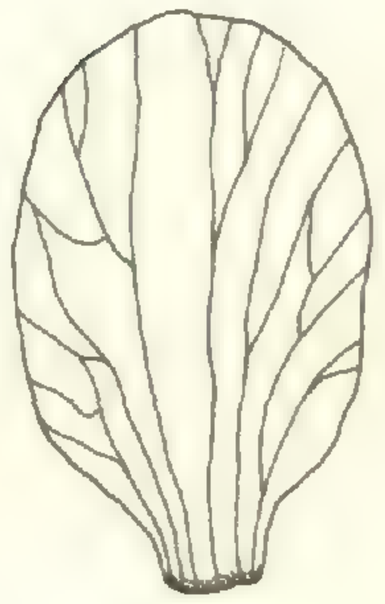
Centradenia rosea Lindley, Bot. Reg. **29**: 20. 1843. TYPES apparently described from cultivated material originally collected at some unknown locality in Mexico. No type specimen can be located. (Lectotype: *pl. 20* of the protologue.)

Centradenia divaricata Kl. in Otto & Dietr. Allg. Gartenz. **19**: 354. 1851. TYPE: Central America, without further locality, *Warscewicz s.n.* (holotype: B, destroyed during World War II, photograph: GH!).

Centradenia oerstediana Kl. in Otto & Dietr. Allg. Gartenz. **19**: 354. 1851. TYPE: Costa Rica, at Turrialba, *Oersted s.n.* (holotype: presumably at B and destroyed during World War II).

Centradenia inaequilateralis var. *major* Cogn. in DC. Monogr. Phan. **7**: 117. 1891. TYPE: Mexico, Rio de Tanetze, *Galeotti 2963A* (holotype: BR; isotypes: F!, NY!, US!).

Erect, flimsy, arcuately branched, suffrutescent perennial 6 cm.–1 m. tall. Distal cauline internodes indistinctly quadrangular, becoming terete and inconspicuously striate in age. Nodal and internodal trichomes typically appressed-strigose but sometimes antrorsely spreading, smooth, mostly less than 0.5 mm. long, white to pink on juvenile growth but often turning tawny-brown with age. Plants anisophyllous. Principal leaves entire, basally oblique, subsessile or tapering to a petiole 0.5–4(–7) mm. long and 0.5 mm. wide, dark green or deeply pigmented above and below, randomly beset above with a sparse to copious mixture of appressed to antrorsely spreading trichomes of two lengths, the larger ones mostly 1–1.5 mm. long and the smaller ones usually less than 0.5 mm.; trichomes of the lower foliar surface uniform in length, ± restricted to elevated primary nerves. Larger leaf at each node narrowly lanceolate to subfalcate, 1–5(–7.5) cm. long and 2–15(–20) mm. wide, attenuate apically, 3-plinerved. Smaller leaf at each node usually early deciduous, linear-oblong, 2.5–8(–14) mm. long and 0.5–3 mm. wide, acute apically, 1-nerved. Inflorescence terminal, but usually on lateral shoots, erect or somewhat pendent, consisting of (1–)2–4(–6) flowers borne on a subfasciculate cluster or short raceme mostly 1 cm. or less in length. Floral bracts sessile, greatly reduced and unlike principal leaves, early deciduous, 0.5–3 mm. long and 0.25–1.0 mm. wide, linear-lanceolate to falcate or narrowly spatulate, glabrous, entire but fringed apically with 3–5 smooth trichomes. Pedicels 1–8(–12) mm. long, mostly erect but becoming strongly cernuous in fruit. Hypanthia (at anthesis) campanulate, sparsely



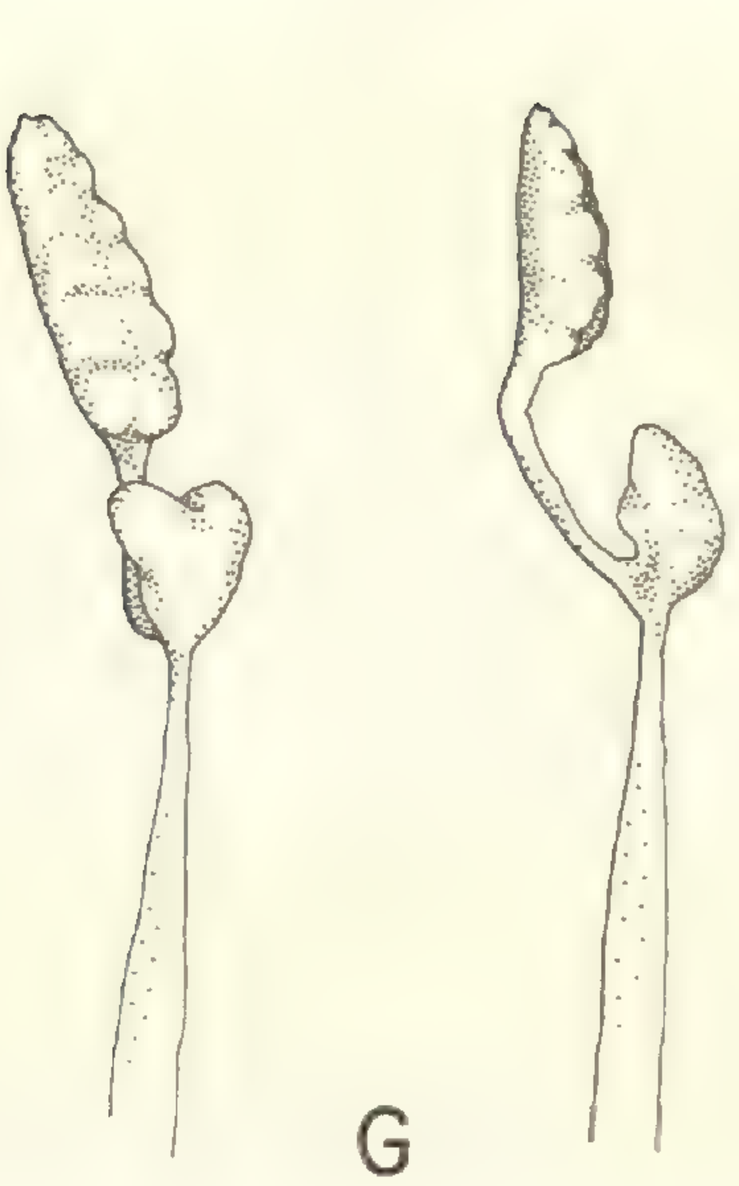


FIGURE 5. **Centradenia inaequilateralis.** A, habit, showing racemose and subfasciculate inflorescences, × ⅓; B, seeds, × 16; C, representative leaves, abaxial surface showing three elevated nerves (left) and adaxial surface (right), × 1; D, petal, × 5; E, mature hypanthium, × 6; F, larger stamens, lateral view showing prolonged connective and obtriangular appendage (left) and ventral view, × 10; G, smaller stamens, lateral view (right) and ventral view (left), × 15. (A–C, E from *Almeda 413*; D, F, & G from *Stone & Welden 3436*).

beset with antrorsely to widely spreading, flexuous trichomes 0.5–1.5(–2.0) mm. long, occasionally bearing additional crystalline bacilliform excrescenses. Sepals (on mature hypanthia) erect, deltoid to ovate-triangular, glabrous within, sparsely pubescent without, ciliate, and tipped with a trichome equaling or exceeding the sepal proper, 1–1.5(–3) mm. long, 1.5–2(–3) mm. wide. Petals white, often fading to pale pink, glabrous, oval to narrowly obovate, sometimes fringed with glandular trichomes, 4–7(–9) mm. long, 2.5–5 mm. wide. Stamens dimorphic. Larger stamens: geniculate, filaments 2.5–4 mm. long; anthers pink, linear-oblong, 1–3 mm. long and 0.5 mm. wide, thecae undulate; connective 1–2.5 mm. long; appendages yellow, erect to ascending-obconic, barely emarginate to bilobed apically, 1.5–2.5 mm. long, 1 mm. wide distally. Smaller stamens: erect or ascending, filaments 2.5–3.5 mm. long; anthers pale yellow, linear-oblong to ovoid, 0.5–1 mm. long, 0.5 mm. wide, thecae gently undulate; connective 0.5–1 mm. long, appendage yellow, erect, ellipsoid to obconic, shallowly bilobed apically, 0.5 mm. long, 0.5 mm. wide. Pollen 11.2–12.5 μm. in diameter. Ovary ovoid, glabrous basally but apically setose. Style 3–4 mm. long, declinate, and opposing the geniculate whorl of stamens. Hypanthia (at maturity) campanulate, ± quadrangular, often deep red in color, 2–3.5 mm. long, 2–3.5 mm. wide. Seeds narrowly pyriform to clavate, muriculate, mostly less than 0.5 mm. long. Chromosome number: $n = 18$.

Flowering: all year.

DISTRIBUTION. Widespread but localized at elevations of 200 to 1900 meters from southeastern Mexico to north-central Guatemala, east to western and central Honduras and south through central and western Nicaragua, to Costa Rica and Panama.

REPRESENTATIVE SPECIMENS. **Costa Rica.** ALAJUELA: C. R. #9 ca. 7.6 km. n. of Varablanca, *Almeda 413* (DUKE); Piedades de San Ramón, *Brenes 4763* (CR, F, MO, NY); calera de San Ramón, *Brenes 5887* (CR, F, MO, NY); e. slopes of Poás along Hwy. #9, n. of Varablanca, *Luteyn 3891* (DUKE); 2 km. w. of La Marina, Llanura de San Carlos, *Molina et al. 17371* (F, GH, NY, US); n. slope of Cordillera Central, *Skutch 3114* (A, MO, NY, US); San Luis de Zarcero, *Smith 122* (US); near San Ramón, *Tonduz 17844* (CR, GH, MICH, US); ca. 1–9 km. n. of Cinco Esquinas, *Wilbur, Almeda, & Luteyn 15742* (DUKE); ca. 4 mi. n. of Varablanca on road to Sarapiquí, *Wilbur & Teeri 13706* (DUKE, F, MICH, MO). ALAJUELA/HEREDIA BORDER: roadbanks along C. R. #9 ca. 7 km. beyond Varablanca, *Almeda 2652* (LA, US). CARTAGO: road to Siquirres ca. 7.1 km. nw. of road junction at Turrialba, *Almeda 557* (DUKE); trail from grounds of Interamerican Institute of Agricultural Sciences, Turrialba, *Carlson 3353* (F, GH); river bank at Turrialba, *Godfrey 66325* (FSU, MO); pasture overlooking Rio Tambor 3 km. e. of Cachí, *Lent 858* (NY); s. of Las Vueltas, Tucurrique, *Tonduz 13065* (US); bank just west of Santa Cruz ca. 10 mi. nw. of Turrialba, *Wilbur & Teeri 13772* (DUKE, GH, MICH, MO, NY). GUANACASTE: vicinity of Monteverde, *Feinsinger s.n.* (CR); El Silencio Tilarán, *Jimenez 393* (CR, F); Los Ayotes near Tilarán, *Standley & Valerio 45397* (F, US); pasture adjoining main road and Chomogo trail near headwaters of Rio Guacimal above Monteverde, *Stone & Welden 3436* (CR, DS, DUKE, MICH, MO); se. slopes of Volcán Mira-

valles near Rio Naranjo, *Wilbur & Almeda 16618* (DUKE); 5 km. e. of Tilarán above Laguna de Arenal, *Williams & Williams 25098* (LL); ca. 2–5 km. se. of Monteverde, *Burger & Gentry 8724* (CR). HEREDIA: ca. 7 km. beyond Varablanca on road to Puerto Viejo, *Almeda & Flowers 2406* (DUKE); waterfall along road between Varablanca and Cariblanco, *Davidse & Pohl 1277* (CR, MO); 7.1 km. n. of Varablanca on Hwy. #9, *Luteyn 599* (DUKE, F); above La Paz on road from Varablanca to Puerto Viejo, *Stone & Welden 3404* (DUKE); slopes above Rio Para Blanco on lower slopes of Cerro Zurquí ca. 7 km. ne. of San Josecito, *Wilbur & Luteyn 18636* (DUKE). LIMON: Rio Pacuar, Comarca de Limon, *Donnell Smith 6550* (US); open banks near Rio Toro Amarillo in vicinity of Guápiles, *Godfrey 66323a* (FSU, MO). PUNTARENAS: vicinity of Monteverde, *Almeda 664* (DUKE). SAN JOSÉ: C. R. #216 ca. 3–6 km. beyond Las Nubes near Cascajal, *Almeda 2629* (DUKE, F, LA, MO, NY, UC, US); Rio Claro along trail to Guápiles, *Burger 3869* (CR, F, NY, US); La Verbena near Alajuelita, *Tonduz 8913* (CR, F, US); ca. 4–4.5 km. n. of San Isidro de San Jose, *Utley & Utley 406* (DUKE); Alto La Palma ca. 7.5 mi. n. of San Vicente, *Wilbur & Almeda 16679* (DUKE); ca. 12 mi. nne. of San Vicente de Moravia, *Wilbur & Almeda 16880* (DUKE). **Guatemala.** ALTA VERAPAZ: near Finca Sepacuite, *Cook & Griggs 222* (US, photo at F); trail from Senahú to Actala, *Maxon & Hay 3336* (GH, NY, US); Pantín, below Tamahú, *Standley 70557* (F). BAJA VERAPAZ: brook bank at Finca Civija, *Sharp 4647* (F, MEXU). SAN MARCOS: canyon s. of San Marcos toward Castalia, *Williams et al. 26114* (F). **Honduras.** CORTÉS: Cuyamel, *Carleton 465* (US). COMAYAGUA: Montaña El Cedral, Cordillera Montecillos 20 km. s. of Siguatepeque, *Molina 8031* (F, NY); Quebrada Montanuelas, *Molina 10860A* (F, LL, NY, US). SANTA BARBARA: San Pedro Sula, *Thieme 5229* (F, GH, US). **Mexico.** VERACRUZ: near Orizaba, *Bilimek 211* (GH, NY, US); Valle de Córdoba, *Bourgeau 1964* (ENCB, GH, MICH, MO, NY, US); Córdoba, *Greenman 201* (F, GH, NY, US); Fortín de las Flores, *Kerber 314* (MICH, US); Zacuapan and vicinity, *Purpus 2304* (F, GH, MO, NY, UC, US); barranca de Tenampa, Zacuapan, *Purpus 5805* (UC); region of Santiago Tuxtla, *Sousa 2253* (MEXU); Santa Rosa, municipio de Teocelo, *Ventura 877* (DS, ENCB, LL); El Mirador, municipio de Totutla, *Ventura 5063* (ENCB); Vista Hermosa, municipio de Jilotepec, *Ventura 9625* (ENCB). **Nicaragua.** GRANADA: Volcan Mombacho, *Baker 2450* (A); summit of Mombacho, *Grant 797* (GH, NY); wet trail on Mombacho volcano, *Maxon, Harvey, & Valentine 7762* (US); rain forest on Mombacho, *Narvaez 3926* (GH, MICH, MO, NY, UC); crater rim on Volcan Mombacho, *Wilbur & Almeda 16582* (DUKE). JINOTEGA: San Rafael del Norte, *Miller & Griscom 73* (US). MANAGUA: vicinity of Managua, *Garnier 936* (US); Sierras de Managua, *Grant 1014* (GH, MICH, NY). MASAYA: region of Las Nubes, Sierra de Managua, *Standley & Garnier 8122* (F). MATAGALPA: river course near Jinotega, *Grant 7297* (GH, NY); near El Porvenir, Cordillera Central, *Molina 20525* (DUKE, F, MO, NY); Cerro El Picacho, finca Santa Maria de Ostuma, Cordillera Central, *Williams et al. 29183* (F, GH, NY, US). **Panama.** BOCAS DEL TORO: 5 mi. s. of Junction of Rios Changuinala and Terebé, *Lewis et al. 864* (MO); Rio Terebé between Queb. Treglo and Puerto Palenque, *Kirkbride & Duke 523* (MO, NY). CHIRIQUÍ: w. side of Cerro Pando, *D'Arcy 6652* (MO); 5.2 mi. nw. of El Hato del Volcan, *Luteyn 830* (DUKE, F, MICH); vicinity of El Boquete, *Maxon 5057* (US); forests around Boquete, *Pittier 3040* (F, US). COCLÉ: hills n. of El Valle, *Allen 3907* (GH, MICH, MO, NY, US); hills ne. of El Valle de Antón, *Lewis et al. 1699* (GH, MO, US); El Valle, *Croat 22978* (MO); 2 mi. n. of El Valle, *McDaniel 8288* (DUKE, FSU); w. slopes

of Cerro Pajita in crater of El Valle de Antón, *Wilbur & Almeda 15609* (DUKE, MO).

This is the most widespread and frequently collected species. As noted by Standley and Williams (1963), although it is surprisingly uncommon through most of its range, it appears to be especially abundant in Costa Rica: over half of the approximately 300 specimens examined are from that country.

Centradenia inaequilateralis exhibits some intricate patterns of variation with respect to such features as stature, pubescence, foliar size, and the degree to which the asymmetry of foliar bases is expressed. Variation involving these characters often occurs in combinations that give individuals or populations a distinctive facies. Despite previous attempts to catalogue this variability, there is no justification for taxonomic fragmentation at any level since none of the variants can be correlated with any consistent geographical or ecological pattern. A few of the variants are sufficiently distinct or recur with ample frequency, however, to warrant brief mention. The variety *major* described from Mexico by Cogniaux, has unusually large, thin leaves, mostly 6.4–7.5 cm. long and 1.7–2 cm. wide, with a sparse and inconspicuous trichome covering. This form appears to be nothing more than an environmentally induced modification since comparable individuals growing under highly shaded conditions have been noted at disjunct localities in Costa Rica and Panama. At the other end of the spectrum, conspicuously dwarfed variants have been found in central Panama (*Lewis et al. 1699*). These variants, collected along the edge of disturbed forests, range in height from 4–15 cm. and have very short internodes, with leaves barely exceeding 2 cm. in length. Similar individuals have also been gathered in central Costa Rica (*Wilbur & Almeda 16880*), where they were found growing epipetrically along a stream bank. Whether these dwarfed variants represent a genetic race remains to be demonstrated, but the array of intermediates bridging them with the larger-leafed forms mentioned above suggests that much of the variation is habitat-mediated.

Another distinctive variant with copious, spreading pubescence on the leaves, stems, and hypanthia is known from Nicaragua (*Grant 7297*) and Costa Rica (*Wilbur & Almeda 16618*). This variation may well have a simple genetic basis comparable to that described elsewhere for *Monochaetum floribundum* (Schlechtd.) Naud. and is perhaps nothing more than a sporadically occurring biotype (Almeda, 1975).

Aside from its simple inflorescence, comparatively small leaves, and diagnostic staminal features, *C. inaequilateralis* can be distinguished from its congeners by the ± quadrangular hypanthia beset with flexuous trichomes. One anomalous collection from Nicaragua (*Miller & Griscom 73*) has hypanthia with narrowly winged angles reminiscent of the mature hypanthia in several species of the South American genus *Pterogastra.* Although this character has been much used as a taxonomic character in

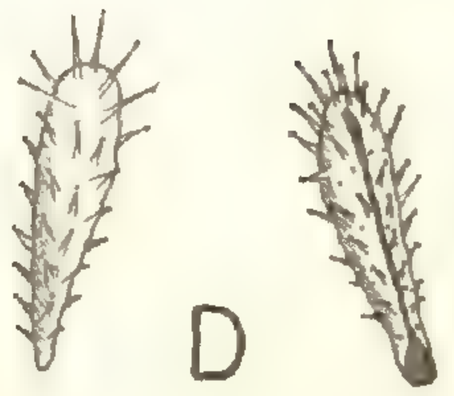
Pterogastra, it appears to be nothing more than a developmental aberration in *Centradenia*.

2. Centradenia paradoxa (Kränzlin) Almeda, comb. nov. FIGURE 6.

Tibouchina (?) *paradoxa* Kränzlin, Vierteljahr. Naturf. Gesell. Zürich **76:** 147. 1931. TYPE: Costa Rica, Bords du Rio Naranjo, Versant Pacifique, 200 m., March 1893, *Tonduz 7628* (holotype: presumably at B and destroyed during World War II; isotypes: F!, GH!, US!).

Centradenia maxoniana Gleason, Bull. Torrey Bot. Club **65:** 571. 1938. TYPE: Panama. Chiriquí: between Hato del Jobo and Cerro Vaca, 700–1000 m., *Pittier 5414* (holotype: US!, photograph: NY!).

Erect, laxly branched shrub or subshrub 0.5–2(–3) m. tall with slender, ± zigzag, flexuous stems. Cauline internodes terete to subquadrangular, copiously beset with appressed, smooth, subulate trichomes (1.0–1.5 mm. long), often intermixed with or replaced by antrorsely spreading, glandular trichomes (0.5–1.0 mm. long) on juvenile growth. Plants strongly anisophyllous. Principal leaves entire, basally asymmetric, dark green above, paler below. Larger leaf at each node linear-lanceolate to somewhat falcate, (4–)5–18 cm. long and 1–3.5(–4.5) cm. wide, acute to attenuate apically, 3–5-plinerved, the three central nerves prominent below, the marginal pair usually depressed and inconspicuous, randomly beset with appressed, smooth trichomes (0.5–1.0 mm. long) on and between impressed primaries on both surfaces, subsessile or with petioles 1–4(–6) mm. long and 1–2(–3) mm. wide. Smaller leaf at each node mostly early deciduous, sessile, narrowly subulate to acicular or falcate, 7–13 (–15) mm. long and 0.5–1.0 mm. wide, sparsely pubescent to glabrate. Inflorescence terminal, commonly on lateral shoots, typically a pendent or nodding, multiflowered, variously reduced dichasium mostly 4–15 cm. long, peduncles ± quadrangular, glandular-pubescent. Floral bracts sessile, thinly membranaceous and translucent, markedly reduced in size upward, early deciduous, 1.5–7(–9) mm. long and 1–3 mm. wide, linear-lanceolate to subulate, often navicular and sheathing immature buds or their pedicels, entire, glandular-puberulent. Pedicels 1.5–5 mm. long, usually cernuous at anthesis bringing the flowers to an inverted position, beset with trichomes like the peduncles of the inflorescence. Hypanthia (at anthesis) cylindric-campanulate, beset with simple and/or glandular, antrorsely spreading trichomes mostly less than 0.5 mm. long. Sepals (on mature hypanthia) erect, ± triangular, varying to depressed-ovate, glabrous within, sparsely puberulent to glabrous without, remotely ciliate, 1–1.5 mm. long and 1–2 mm. wide at base. Petals white, linear-oblong to narrowly obovate, entire, glabrous but minutely glandular-ciliate, 5–7 mm. long and 3–4 mm. wide. Stamens subequal, alternately differing in length, straight, ± connivent around the style; thecae yellow, linear-subulate, markedly convoluted and channeled ventrally along the connective which is modified basally (at point of filament insertion) into a dilated, facially flattened, triangular spur or tubercular appendage.



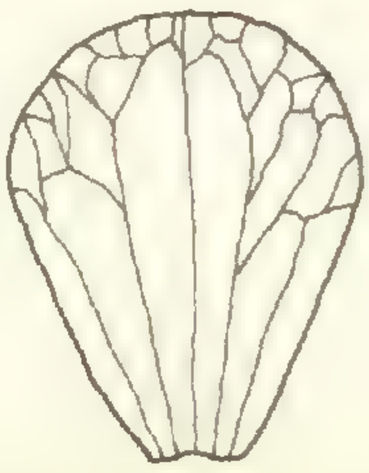


FIGURE 6. **Centradenia paradoxa.** A, habit, × ⅓; B, smaller stamen, ventral view, × 8; C, larger stamen, lateral view, × 8; D, seeds, dorsal view (left) and ventral view (right), × 30; E, petal, × ca. 3; F, leaf, adaxial surface, × ½; G, mature hypanthium, × 4; H, leaf, abaxial surface, × ½. (A, F, H from *Allen 112*; B–E, G from *Wilbur & Almeda 15607*).

Larger stamens: filaments 2–3.5 mm. long; anthers 3–4 mm. long and 0.5 mm. wide; connective and appendage each 0.5–1.0 mm. long. Smaller (antepetalous) stamens: filaments 1–2.5 mm. long; anthers 2–3.5 mm. long and 0.5 mm. wide; connectives and appendages like those of larger stamens. Pollen 11.2–12.5 μm. in diameter. Ovary ovoid to obovoid, glandular-ciliate at the summit but otherwise glabrous. Style slender, 6–8 mm. long, equaling or exceeding the larger stamens, straight and terminated by a subcapitate stigma. Hypanthia (at maturity) 4–7 mm. long, 3–6 mm. wide. Seeds clavate, usually less than 0.5 mm. long, covered with numerous glandular setose projections. Chromosome number: $n = 18$.

Flowering: December–March.

DISTRIBUTION. Puntarenas and San José provinces on the Pacific side of the Cordillera de Talamanca in southwestern Costa Rica, extending southeastward in disjunct fashion to Chiriquí and Coclé provinces in Panama and south to the Chocó lowlands of Colombia, from sea level to 1200 meters.

REPRESENTATIVE SPECIMENS. **Colombia.** CHOCÓ: Alto de Buey, *Gentry & Forero 7291* (MO); along stream at Bahia Solano, *Haught 5529* (NY, US). **Costa Rica.** PUNTARENAS: Cienega de Cañas Gordas, *Pittier 11061* (CR, US). SAN JOSÉ: C. R. #223 ca. 16–24 km. s. of San Isidro del General, *Almeda 2692* (F, GH, LA, US), *Almeda 2693* (DUKE, LA, MICH, MO, NY, US); 20 km. w. of San Isidro del General, *Davidse & Pohl 1293* (MO, US); Alto La Palmera, Carretera Panamericana, *Jimenez 3741* (CR); vicinity of El General, *Skutch 3964* (A, MO, NY, US); basin of El General, *Skutch 4690* (A, CR, F, MO, NY, US). **Panama.** CHIRIQUÍ: eastern Chiriquí between Hato del Jobo and Cerro Vaca, *Pittier 5414* (US, photo at NY). COCLÉ: vicinity of El Valle along the lower Rio Antón, *Allen 112* (A, MO, NY); El Valle, *Allen 1175* (GH, MO, NY, US); w. slopes of Cerro Pajita in crater of El Valle de Antón ca. 3 mi. n. of El Valle, *Wilbur & Almeda 15607* (DUKE, MICH, MO); Bismark above Penonomé, *Williams 321* (NY, US).

This species exhibits little intraspecific variation in features that tend to be plastic in other taxa. The pendent flowers, straight styles, connivent, linear-subulate anthers, and greatly reduced appendages differ so markedly from other congeners that Kränzlin's initial placement of this entity in *Tibouchina* is understandable. *Centradenia paradoxa* superficially resembles *Tibouchina longifolia* (Vahl) Baillon ex Cogniaux in habit and floral features, but the latter differs consistently in having 5-merous flowers, linear-lanceolate sepals, cochleate seeds, symmetric leaf bases, and adaxial foliar trichomes which are adnate to the epidermis for a portion of their length.

Kränzlin was correct in expressing doubt over the generic assignment of his new species since the specimens known to him lacked mature capsules and seeds. The slender, more or less zigzag stems and caducous nature of the smaller leaf at each node led him erroneously to suggest, however, that this species might be a woody climber with alternate phyllotaxy.

Williams (1963) emphasized the overall similarity of this species to

Centradenia inaequilateralis and suggested that it represented nothing more than a large-leafed variant of the latter, perhaps worthy of infraspecific status. Field studies of these taxa leave no doubt that they should be retained as distinct species. They differ dramatically in several characters, the most notable being foliar size, floral bracts, inflorescences, hypanthia, stamens, and seeds.

The closest relative of *C. paradoxa* appears to be *C. grandifolia* subsp. *grandifolia* with which it shares clavate, echinate seeds and a more or less dichasial inflorescence.

3. **Centradenia floribunda** Planchon, Fl. Serres **5**: *pl. 453.* 1849.

Erect, laxly branched, suffrutescent perennial mostly (12–)20–50 cm., but infrequently as tall as 1.5 m. Cauline internodes terete to subquadrangular, glabrate below but moderately to copiously appressed-pubescent above, the trichomes either smooth or glandular, and prevailingly less than 0.5 mm. long. Principal leaves dimorphic to subequal in each pair, entire, lanceolate, apically acute to attenuate, basally symmetric and attenuate or somewhat oblique, moderately to sparsely appressed-pubescent above with trichomes often restricted to the elevated primary nerves below. Larger leaf at each node 2–10 cm. long and 0.5–3.5 cm. wide, 3–5-plinerved, the three central nerves elevated and conspicuous below, the marginal pair mostly depressed and inconspicuous; petioles 0.8–2.5(–4) cm. long and 1 mm. wide. Smaller leaf at each node usually persistent, 0.5–6 mm. long and 0.5–1.0 mm. wide. Inflorescence terminal, often on lateral shoots, basically paniculate in outline but typically consisting of a cluster of 2–6 elongate racemes diverging from one another ± basally. Floral bracts thinly membranaceous, reduced in size upward along the raceme, early deciduous, 2–10 mm. long, 0.5–3 mm. wide, linear-lanceolate to obovate, entire, glabrous within and puberulent without, uppermost bracts closely enveloping buds or their pedicels. Pedicels 4–9 mm. long, glandular-puberulent, erect at anthesis but strongly cernuous in fruit. Hypanthia (at anthesis) campanulate, beset with a copious mixture of smooth, appressed, and spreading glandular trichomes. Sepals (on mature hypanthia) erect, broadly deltoid and apically rounded, glabrous within and glandular-puberulent without, 1–2 mm. long and 1.5–2 mm. wide. Petals pale pink to magenta, obovate, entire, sometimes remotely ciliate and shallowly emarginate, 4–11 mm. long and 3.5–9 mm. wide. Stamens strongly dimorphic, alternately dissimilar with prolonged connectives modified ventrally into elaborate upturned appendages, or stamens weakly dimorphic with short connectives and markedly reduced appendages. Pollen 12.5–15 μm. in diameter. Ovary obovoid, glabrous or sparingly beset with smooth and/or glandular trichomes; the wall elaborated apically into eight compressed, ± triangular gland-tipped lobes surrounding the stylar base. Style straight or declinate, 4–8 mm. long, stigma punctiform to subcapitate. Hypanthia (at maturity) campanulate to suburceolate, 3–5 mm. long and 2.5–4 mm. wide. Seeds narrowly pyriform to clavate, muriculate to obscurely papillate, mostly 0.5 mm. long.

As presently perceived, *Centradenia floribunda* consists of two allopatric entities herein accorded subspecific recognition. Indistinguishable on vegetative grounds, these taxa are based largely on diagnostic floral characters involving the size, shape, and orientation of anther thecae, connectives, ventral appendages, and style. Williams (1963), on the basis of the limited material then available, indicated that some specimens appeared to be intermediate between the two floral types. My study of this species complex has included all specimens examined by Williams plus collections from additional populations that have accumulated in the interim. Since all specimens are readily assignable to one subspecies or the other, I feel that failure to draw a formal distinction between them would obscure evolutionary tendencies. Unfortunately, this is the only species that has not been studied in the field: the adaptive significance of the geographically correlated floral dimorphism is, therefore, not clear at this time. By extrapolating from what is known about the floral biology of the other species, one may predict that the floral peculiarities are correlated with modally different pollination systems.

3a. Centradenia floribunda Planchon subsp. floribunda. FIGURE 7.

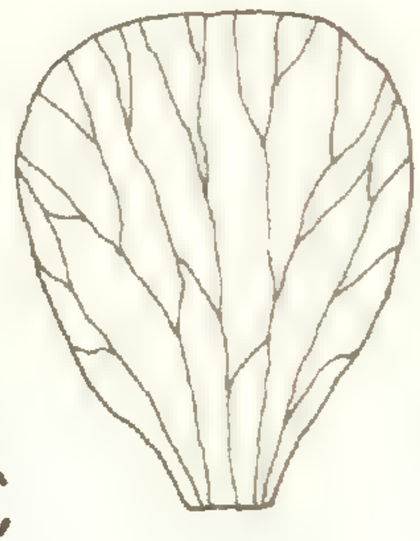
Centradenia floribunda Planchon, Fl. Serres **5**: *pl. 453.* TYPE: although no type has been either designated or located, I gather from the protologue that this species was described from cultivated material grown from seed that was presumably collected at an unknown locality in Guatemala (lectotype: unnumbered colored plate opposite page 453 of the protologue).

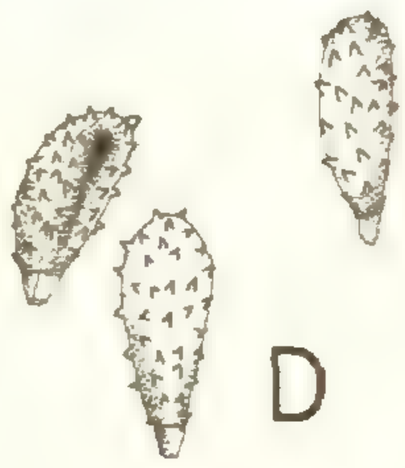
Centradenia floribunda Planchon var. *grandifolia* Cogniaux in Donn. Sm. Bot. Gaz. **20**: 286. 1895. TYPE: Guatemala. Amatitlan: Palin, *Donnell Smith 2645* (holotype: US!; isotypes: F!, GH!, NY!).

Petioles of larger leaf at each node 0.4–1.5(–2.5) cm. long. Petals pale pink, 4–7 mm. long and 3.5–5 mm. wide. Stamens weakly dimorphic to subequal, alternately differing in length, straight or slightly flaring distally and ± connivent around the style. Larger stamens: filaments 3–4 mm. long; anthers pale yellow, elliptic to elliptic-obovate, 1–1.5 mm. long, 1 mm. wide, thecae smooth and not conspicuously convolute; connective 1 mm. long; appendages yellow, compressed, bilobate or trilobate, upturned or deflexed, 0.5–1.0 mm. long and ± 0.5 mm. wide. Smaller stamens: filaments 3–3.5 mm. long; anthers pale yellow, ovate to elliptic-ovate, 1–1.5 mm. long, 0.5 mm. wide, thecae smooth, channeled ventrally; connective 0.5 mm. long; appendages yellow, shallowly bilobed, mostly less than 0.5 mm. long. Style straight, 4–6 mm. long, ± equaling the stamens. Chromosome number: $n = 18$.

Flowering: all year.

DISTRIBUTION. From Volcán Tacaná in eastern Chiapas, Mexico, to the western and central departments of Guatemala, mostly at elevations of 250 to 1800 meters but infrequently as high as 2450 meters. The type collection of *Centradenia floribunda* var. *grandifolia* was reportedly collected at an elevation of 3560 meters. This is questionable and requires





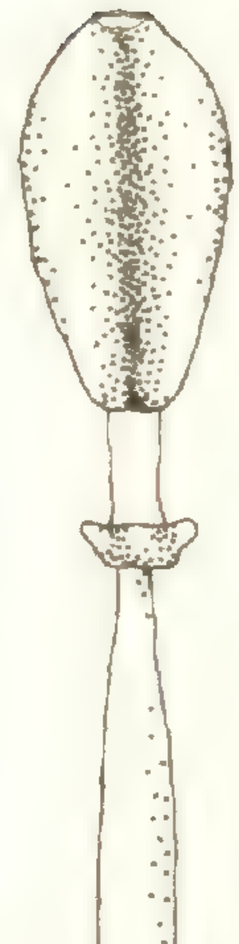


FIGURE 7. **Centradenia floribunda** subsp. **floribunda.** A, habit showing anisophylly, × ca. ⅓; B, larger stamens, lateral view (left) and ventral view (right), × 20; C, petal, × 4; D, seeds, × 24; E, smaller stamens, lateral view (left) and ventral view (right), × 15; F, mature hypanthium, × 5; G, leaves, abaxial surface (left) and adaxial surface (right). (A–G from *Stone 3092*).

additional collections for confirmation. One other specimen, *Schaffner s.n.* (A) was purportedly collected at Santa Ana in Jalisco, Mexico, a locality unknown for the genus and far removed from the normal range of this species. If the label data on that collection are correct, it would constitute an appreciable westward range extension for *C. floribunda* since it is not known in Mexico from any intervening area west of Volcán Tacaná on the Guatemalan border. Although a few species of flowering plants are known from Jalisco and not otherwise except from Central America or the West Indies (McVaugh, pers. comm.), I am inclined to doubt the authenticity of this record until it is substantiated by recent collections.

REPRESENTATIVE SPECIMENS. **Mexico.** CHIAPAS: Volcán Tacaná, *Matuda 2751* (MEXU, MICH, NY). **Guatemala.** CHIMALTENANGO: Concepción, *Johnston 534* (F). CHIQUIMULA: vicinity of Montaña Cebollas, along Rio Lucia Saso ca. 3 mi. se. of Quezaltepeque, *Steyermark 31318* (F). ESCUINTLA: vicinity of Escuintla, *Donnell Smith 2216* (F, GH, MO, NY, US); 1–5 km. e. of CA-9 on road to San Vicente Pacaya, *Harmon 1946* (ENCB, MO); cliffs about Finca Zapote, *Muenscher 12341* (F); along Rio Guacalate, *Standley 58161* (F, NY); between Rio Jute and Rio Pantaleop on road between Escuintla and Santa Lucia, *Standley 63436* (F, NY). GUATEMALA: near finca La Aurora, *Aguilar 222* (F); sand creek ca. 12 mi. ne. of Guatemala City, *Brenckle 47397* (F, NY); banks along Rio Villalobos, *Molina, Burger, & Wallenta 16031* (F, NY, US); arroyo s. of Guatemala on road to Amatitlan, *Standley 62817* (F, MICH, NY). JALAPA: Los Chorros along Rio Pinule ca. 1 mi. w. of San Pedro Pinula, *Steyermark 32936* (F, NY); between Jalapa and La Laguna, *Standley 76899* (F). QUEZALTENANGO: off Hwy. 95 at km. 197, old road to Finca Pirineos, *Stone 3092* (DUKE); lower south-facing slopes of Volcan Santa María between Finca Pirineos and Finca Soledad, *Steyermark 33568* (F); damp thickets near Colomba, *Standley 67983* (F); roadside bank, finca Helvetia, *Skutch 1404* (GH, NY); San Martin, *Shannon 513* (US). QUICHÉ: Cunen, *Heyde & Lux 3332* (MO, US). RETALHULEU: Ajaxa e. of Santa Cruz Mulua, *Standley 88206* (F); along road 5 km. w. of Retalhuleu, *Standley 87353* (F, NY); La Llovizna, *Rojas 232* (MO, US); vicinity of San Felipe, *Maxon & Hay 3535* (NY, US); along Rio Samala, *Donnell Smith 2651* (MO, US). SACATEPEQUEZ: near Las Lajas, *Standley 58143* (F, NY). SANTA ROSA: Teocinte, *Heyde & Lux 4181* (GH, NY, US); Aguacaliente, *Kellerman 7760* (US); vicinity of Chiquimulilla, *Standley 79537* (NY). SUCHITEPEQUEZ: finca El Naranjo, s. slopes of Volcan Santa Clara, 12 km. sw. of Volcan Santa Clara, 12 km. sw. of Lago Atitlan, *Fosberg 27187* (US); near bridge on CA-2 along Rio Mora, *Harmon & Dwyer 3411* (ENCB, MO); vicinity of Mazatenango, *Maxon & Hay 3458* (US); rocky banks at Finca Moca, *Skutch 2065* (F, GH, NY); near Pueblo Nuevo, *Standley 66842* (F); south-facing slopes and barrancas of Volcan Santa Clara, *Steyermark 46790* (F, GH, NY, US).

This subspecies varies markedly in foliar size, number of flowers per inflorescence, and the amount of pubescence on the leaves, cauline internodes, and inflorescences. Large-leafed forms from Amatitlan and Retalhuleu, Guatemala, have been recognized as variety *grandifolia*, but these grade imperceptibly into the typical forms from the same localities and appear to be unworthy of taxonomic status. The distinctive staminal features of this taxon should preclude confusion with all other species. Sterile,

depauperate specimens occasionally approach *C. inaequilateralis* in leaf size and shape, but that species differs in its pronounced anisophylly and size mixture of adaxial foliar trichomes.

3b. **Centradenia floribunda** Planchon subsp. **bernoullii** (Cario ex Cogn.) Almeda, comb. nov. FIGURE 8.

Centradenia bernoullii Cario ex Cogn. DC. Monogr. Phan. **7:** 118. 1891. TYPE: El Salvador, without further locality, *Bernoulli 2* (holotype: B, destroyed during World War II, photographs: GH!, NY!; syntypes: presumably at GOET, K).

Centradenia floribunda Planchon var. *bernoullii* (Cario ex Cogn.) L. O. Williams, Fieldiana Bot. **29:** 552. 1963.

Centradenia perquinensis S. Winkler, Bot. Jahrb. **83:** 343. 1965. TYPE: El Salvador. Morazan: Feuchte Bachschlucht am Zompopero an der Strasse Perquin–Savanetas, *Winkler s.n.* (holotype: herbarium of S. Winkler at TUB; isotypes: F!, ITIC).

Petioles of larger leaf at each node 0.8–2.5(–3.5) cm. long. Petals 7–11 mm. long and 4–9 mm. wide. Stamens strongly dimorphic. Larger stamens: geniculate, filaments declinate, 4.5–6.5 mm. long; anthers deep pink to magenta, linear-oblong, 2.5–3 mm. long, 1 mm. wide, thecae distinctly undulate ventrally; connective 2–3 mm. long; appendages yellow, compressed and ligulate or slightly dilated, linear-oblong to ± obtriangular, apically erose with two terminal, upturned, caudiform processes, 3.5–5 mm. long and 1–1.5 mm. wide. Smaller stamens: ± erect to somewhat incurved, filaments 4–6 mm. long; anthers yellow, linear-oblong, 1.5–2 mm. long, 0.5 mm. wide, thecae undulate; connective 1 mm. long; appendages yellow, ± compressed, narrowly obtriangular and distinctly bifurcate, 1 mm. long. Style declinate, 6.5–8 mm. long, ± opposing the apical pores of the larger stamens.

Flowering: December to January, and perhaps sporadically during other months.

DISTRIBUTION: Sporadic through much of El Salvador, extending north to western and central Honduras, at elevations of 350 to 1800 meters.

REPRESENTATIVE SPECIMENS. **El Salvador.** AHUACHAPAN: vicinity of Ahuachapan, *Standley 20282* (NY, US); *Standley & Padilla 2504* (F); Laguna de las Ninfas near Apaneca, *Winkler s.n.* (F). CUSCATLAN: Cojutepeque, *Shannon 5035* (F, GH, US). LA LIBERTAD: vicinity of Santa Tecla, *Standley 23056* (GH, US); s. of Santa Tecla, *Williams & Molina 15093a* (F); moist bank above Colon, *Williams & Molina 16784* (F). MORAZAN: s. side of Montes de Cacaguatique, *Tucker 745* (F, MICH, UC, US). SAN SALVADOR: vicinity of San Marcos, *Carlson 1* (F, GH, NY, UC, US); El Picacho, Volcan San Salvador, *Molina & Montalvo 21864* (DS, GH, NY). SAN VICENTE: vicinity of San Vicente, *Standley 21210* (GH, US); *Standley & Padilla 3402* (F). SONSONATE: vicinity of Izalco, *Pittier 1945* (US); vicinity of Armenia, *Standley 23479* (GH, NY, US). **Honduras.** COMAYAGUA: Barranco Trincheras ca. 16 km. from Siguatepeque, *Molina 7936* (F); Quebrada Montanuelas between Trincheras and Montanuelas, *Molina*

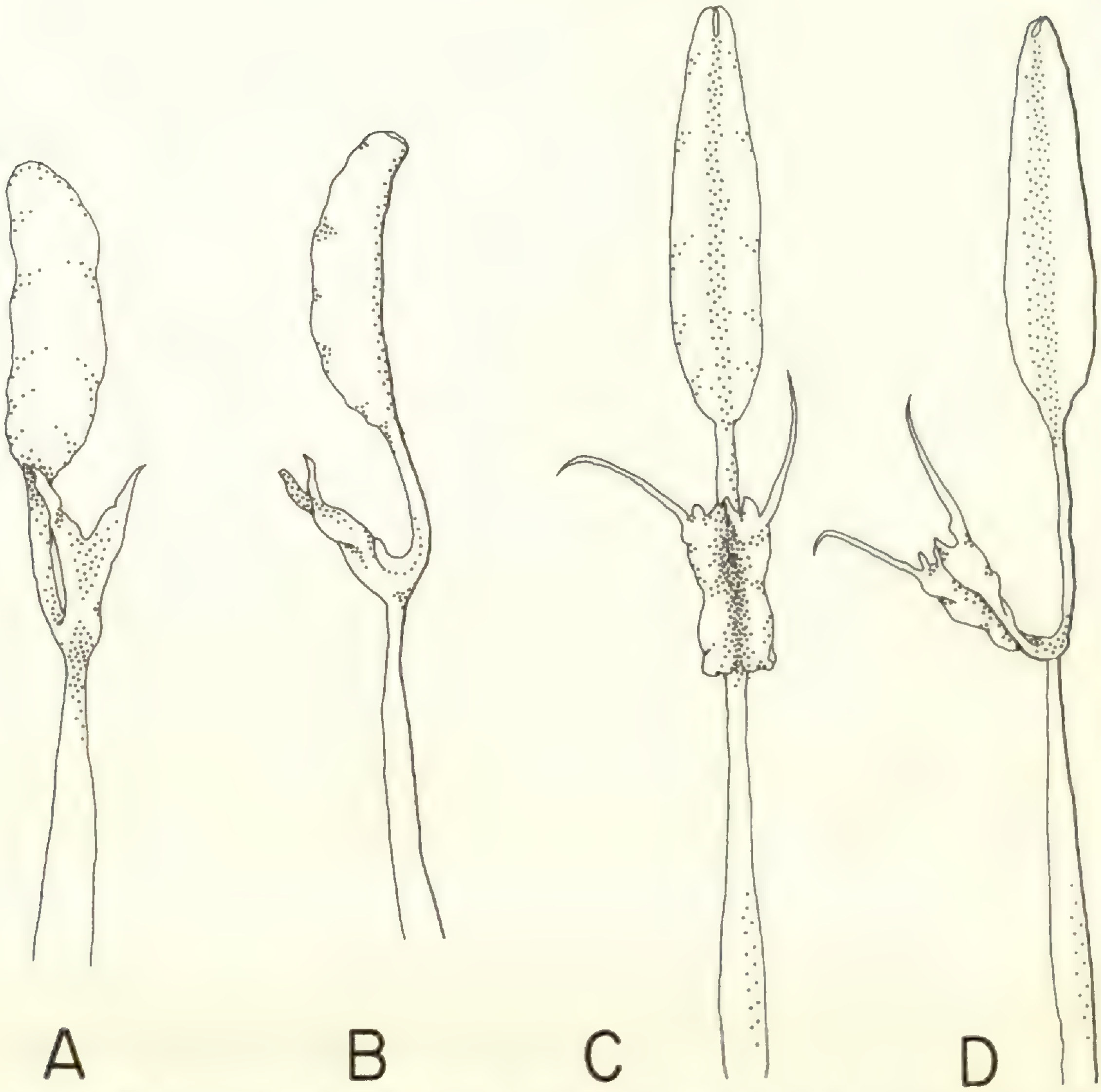


FIGURE 8. **Centradenia floribunda** subsp. **bernoullii.** A & B, smaller stamens, ventral view (left) and lateral view (right), × 14; C & D, larger stamens, ventral view (left) and lateral view (right) showing setose appendage, × 14. (A–D from *Molina & Montalvo 21864*).

10860A (US); La Cocona, 6 km. e. of Siguatepeque, *Molina & Molina 25489* (F, NY); vicinity of Siguatepeque, *Standley 55910* (F, US); 5 km. s. of La Mision, *Williams & Molina 18004* (GH, US); ravine near El Achote above plains of Siguatepeque, *Yuncker et al. 6614* (F, GH, MICH, MO). EL PARAÍSO: Barranco Galeras between Casitas and Cuesta de Galeras, *Molina 8571* (F, US); Quebrada Tapahuasea between Manzaragua and San Lucas, *Molina 18737* (F, NY); Guinope, *Rodriguez 1827* (F). INTIBUCÁ: Cascada de Yamaranguila, *Molina 6344* (F, NY, US); Cordillera Opalaca, between El Pelon and Camaco on road to Gracias, *Molina & Molina 24457* (F); 9 km. e. of La Esperanza along Huise River, *Molina & Molina 25564* (NY). LA PAZ: between Florida and El Cerron ca. 7 km. from Marcala, *Molina 24072* (DS, F); between Sasagua River and Llano de San Antonio, *Molina 24131* (F, NY). MORAZAN: vicinity of Las Mesas, *Swallen 11422* (US); along Quebrada Quemada at km. 21 in vicinity of Cerro de Hule, *Molina 25417* (DUKE, F, MO).

This subspecies is characterized by its linear-oblong anthers, prolonged connectives, and unique staminal appendages. Foliar size appears to be the only character that displays any notable variation. In general, the Honduran populations have narrower linear-lanceolate leaves with symmetric bases that appear very different from the typical element. Although narrow-leafed forms are less frequent in El Salvador, at least one such collection from Morazan formed the basis for Winkler's *Centradenia perquinensis*, a species herein relegated to synonymy.

One unusual collection from the vicinity of Apaneca, El Salvador (*Winkler s.n.*), has narrowly winged, cauline internodes, a rather congested paniculate inflorescence, and large fruiting hypanthia reminiscent of *C. grandifolia*, but the floral and seed characters leave no doubt that it should be assigned to this subspecies.

While there is no strong evidence to suggest which of the subspecies is the most "primitive," I have intuitively favored subspecies *bernoullii* as the most likely candidate. Evolution of the comparatively simple structure and conformation of stamens in subspecies *floribunda* is easily envisaged by a reduction of anthers, connectives, and appendages, coupled with a change in their posture and orientation.

4. **Centradenia grandifolia** (Schlechtd.) Endl. Rep. Bot. Syst. 2: 119. 1843.

Erect, strictly to arcuately branched, suffrutescent perennial, 0.5–1.5 m. tall. Distal cauline internodes semisucculent, strongly quadrangular and conspicuously alate, glabrate to puberulent, the trichomes appressed to spreading, and mostly less than 0.5 mm. long. Plants strongly anisophyllous. Principal leaves thinly membranaceous, entire, basally asymmetric, dark green above and often deeply pigmented below. Large leaf at each node lanceolate to ovate-lanceolate, typically appearing broadly falcate, (2–)5–20(–24) cm. long, 1.5–7 cm. wide, apically acute to acuminate or attenuate, (4–)5–6(–7)-plinerved with a conspicuous network of secondary veinlets, sparsely to copiously pubescent above, but trichomes largely confined to primary and secondary nerves below; petioles 1–13(–22) mm. long, sometimes alate, the wings often extending along the median nerve for ½–⅔ the length of the blade. Smaller leaf at each node commonly deciduous, sessile, narrowly lanceolate to falcate or subulate, 1–12(–25) mm. long and 1–7 mm. wide, glabrous above and puberulent to glabrate below. Inflorescence terminal or axillary, typically a multiflowered (often corymbiform) dichasium 7–18 cm. long, peduncles glabrate or beset with both smooth and glandular trichomes. Floral bracts sessile, deciduous, 2–18(–33) mm. long and 0.5–6 mm. wide, linear-lanceolate to obovate or subulate, enveloping young buds and pedicels, glabrous above, sparsely puberulent below. Pedicels (1–)4–12 mm. long, glabrous or glandular-puberulent. Hypanthia (at anthesis) urceolate to campanulate, glabrous or glandular-puberulent. Sepals (on mature hypanthia) ± erect, triangular-ovate to truncate or mucronulate, entire to remotely crenulate, ciliate,

1–3 mm. long. Petals pink or white, obovate, entire to obscurely erose or crenulate, often fringed with glandular trichomes, 5–11 mm. long, 4–8 mm. wide. Stamens dimorphic. Larger stamens: geniculate; filaments 4.5–7 mm. long, anthers pink to magenta, linear-oblong to subulate, 4–5.5 mm. long and 1 mm. wide, thecae undulate; connective 2–5.5 mm. long; appendages yellow, ± horizontal, clavate, dilated and bluntly bifurcate distally, 1.5–3 mm. long. Smaller stamens: erect; filaments 4–6 mm. long; anthers and appendages yellow, 2–4.5 mm. and 0.5–1 mm. long, respectively, otherwise similar to larger anthers. Ovary ovoid to obovoid, puberulent, the wall elaborated apically into four scalelike outgrowths surrounding stylar base. Style 7–12.5 mm. long, declinate, and opposing the geniculate staminal whorl. Hypanthia (at maturity) 4–8 mm. long and 4–8 mm. wide. Seeds 0.5–1 mm. long, clavate to dolabriform, echinate, muricate, or with low, domelike processes.

The extensive morphological variability exhibited by *C. grandifolia* is comparable to that of *C. inaequilateralis*; unlike that species, it falls into two discontinuous, geographically definable patterns, thus justifying subspecific status. Basic differences between the two subspecies reside in hypanthial and sepal shape, the surface pattern and shape of seeds, and perhaps less significantly in petal color.

4a. Centradenia grandifolia (Schlechtd.) Endl. subsp. **grandifolia.** FIGURE 9 A–E, G–I.

Rhexia grandifolia Schlechtd. Linnaea **13:** 429. 1839. TYPE: Mexico. Veracruz: Cuesta Grande de Chiconquiaco, *Schiede s.n.* (holotype: presumably at B and destroyed during World War II; isotype: NY!).

Centradenia salicifolia T. S. Brandegee, Univ. Calif. Publ. Bot. **4:** 379. 1913. TYPE: Mexico. Veracruz: Sierra Madre between Misantla and Naolinco, *Purpus 6103* (holotype: UC!; isotypes: F!, GH!, MO!, NY!, US!).

Centradenia chiapensis T. S. Brandegee, Univ. Calif. Publ. Bot. **6:** 501. 1919. TYPE: Mexico. Chiapas: Cerro del Boqueron, *Purpus 6978* (holotype: UC!).

Mature hypanthia urceolate, broadest at the middle, 4–8 mm. long, glabrous or glandular-puberulent, accrescent and bladdery, loosely enveloping the ovoid ovary. Sepals triangular-ovate, apically rounded, (1–)2–3 mm. long. Petals pink. Pollen 16.2–17.5 μm. in diameter. Seeds clavate, echinate, the setose projections often appearing glandular. Chromosome number: $n = 18$.

Flowering: all year.

DISTRIBUTION: Hidalgo, Puebla, Veracruz, and Chiapas in southeastern Mexico, to San Marcos, Suchitepequez and Quezaltenango in western Guatemala, with southern disjunct populations in the provinces of Alajuela, Cartago, and San José, Costa Rica, at elevations of 1300 to 2500 meters. Molina (1975) includes this taxon in his enumeration of Honduran plants, but the collection upon which his record was presumably based (*Molina 18738*) matches typical *C. floribunda* subsp. *bernoullii* in all details. To date, I have seen no authentic material of *C. grandifolia* from Honduras.

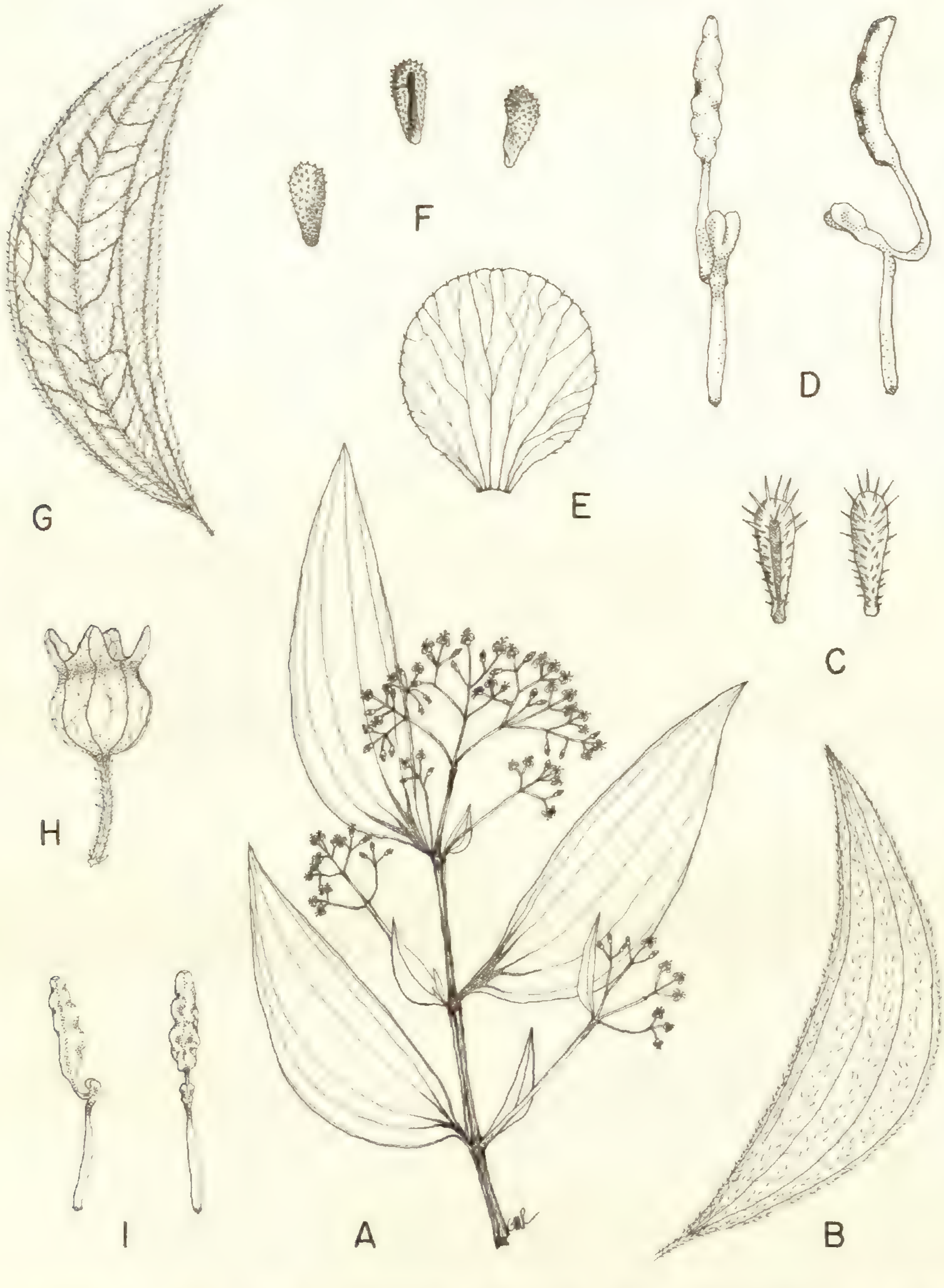


FIGURE 9. A–E, G–I, **Centradenia grandifolia** subsp. **grandifolia.** A. habit, showing quadrangular stem and dichasial inflorescence, × ca. ⅓; B, leaf, showing adaxial surface, × ½; C, seeds, ventral view showing raphe (left) and dorsal view (right), × 15; D, larger stamens, showing prolonged connective and bilobed appendage, ventral view (left) and lateral view (right), × 4; E, petal, × 3. F, **Centradenia grandifolia** subsp. **brevisepala,** seeds, × 11. Subsp. **grandifolia,** G, leaf, showing abaxial surface, × ½; H, hypanthium, × 2; I, smaller stamens, lateral view (left) and ventral view (right), × 4. (A–E, G–I from *Almeda & Flowers 2080*; F, from *Donnell Smith 1540*).

REPRESENTATIVE SPECIMENS. **Costa Rica.** ALAJUELA: Tapesco de Zarcero on road to Quesada, *Smith 251* (US); Zapote de San Carlos, *Smith PC315* (F); vicinity of Naranjo, *Stork 1843* (F, MICH). CARTAGO: ca. 20 km. se. of Cartago, *Godfrey 66136* (FSU); km. 49 on Panamanian Hwy. s. of Tejar, *Lent 262* (F, NY); ca. 6 km. n. of El Empalme towards Cartago, *Wilbur, Almeda, & Luteyn 16190* (CAS, DUKE, F, LL, MICH, MO, US). SAN JOSÉ: ca. 27 km. sse. of Cartago and 51 km. nnw. of Villa Mills, *Almeda 2677* (F, LA, MO, UC, US); ca. 9 km. beyond San Isidro del General, *Almeda & Flowers 2080* (CR, DUKE, F, MICH, MO, UC); 25 km. n. of San Isidro del General, *Burger & Leisner 7051* (CR, NY); 14 km. s. of División, *Davidse & Pohl 1404* (CR, MO, US); vicinity of El General, *Skutch 4205* (A, MO, NY, US); vicinity of Santa María de Dota, *Standley & Valerio 44093* (F, US); 16 mi. n. of San Isidro, *Wilbur & Luteyn 19005* (DUKE, LA). **Guatemala.** QUEZALTENANGO: slopes of Volcan Zuñil above Agual Amargas, *Standley 65325* (F, GH, NY); Cumbre de Tuilacan, sw. of San Martín Chile Verde, *Standley 67764* (F); region of Boxantin, se. of San Martín Chile Verde, *Standley 83759* (NY); along Rio Samala, near Santa María de Jesus, *Standley 84577* (F); above Mujulia, between San Martín Chile Verde and Colomba, *Standley 85451* (F); along Rio Samala, between Santa María de Jesus and Calahuache, *Steyermark 33877* (F, NY). SAN MARCOS: 9.6 mi. w. of San Pedro Sac towards San Rafael Pie de la Cuesta, *Luteyn & Almeda 3474* (DUKE, F); slopes along Rio Vega on ne. portion of Volcán Tacaná near San Rafael, *Steyermark 36343* (F, NY); nw. slopes of Volcán Tajumulco, 6 mi. sw. of Tajumulco, *Steyermark 36644* (F); 5 mi. e. of San Rafael en route to San Marcos, *Whiffin & Rodriguez 430* (TEX). SUCHITEPEQUEZ: sw. slopes of Volcan Zuñil between finca Montecristo and finca Asturias, *Steyermark 35312* (F, NY). **Mexico.** CHIAPAS: Union Juarez, Volcán Tacaná, *Matuda 3001* (F, GH, MEXU, MICH, MO); Tapalapa, Blanca Rosa, *Miranda 6559* (MEXU); Cerro del Boquerón, *Purpus 7059* (GH, NY, UC). HIDALGO: 2 km. s. of Tlanchinol, *Rzedowski & Madrigal 29453* (ENCB). PUEBLA: near summit of El Cerro de Cuhuatepetl ca. 15–16 km. sw. of Campo Experimental de Hule, *Santos 3665* (MICH, US); falls of Necaxa, district of Huauchinango, *Roby s.n.* (US). VERACRUZ: above Canada del Huerfano, *Gómez-Pompa 1822* (MEXU); Cerro Punta Coscomat, *Matuda 1506* (MEXU, MICH); Santa Rita, Sierra de Chiconquiaco, *Nevling & Gómez-Pompa 19* (GH, MEXU); 5 km. s. of Coscomatepec, *Rzedowski 19075* (ENCB, MICH, US); El Haya, municipio de Yecuatla, *Ventura 3286* (ENCB); municipio de Naolinco, *Ventura 10400* (ENCB).

This well-marked subspecies is readily distinguished by its strongly quadrangular to alate stems, dimorphic androecium, urceolate hypanthia, and echinate seeds. The disjunct population structure of this taxon has undoubtedly promoted some inter-populational differentiation. Many of the Costa Rican populations have larger leaves (16–23 × 5–7 cm.), glabrous hypanthia, and denser pubescence on the inflorescence and upper foliar surfaces, but these variations are also displayed by a collection (*Rzedowski & Madrigal 29453*) from the northernmost locality for the species in Hidalgo, Mexico.

Specimens from Chiapas and Veracruz, to which Brandegee assigned specific epithets, undoubtedly belong here but differ from typical plants in their narrower, glabrate leaves and few-flowered inflorescences with shorter internodes.

The most distinctive variant from Puebla, Mexico (*Santos 3665*) has subquadrangular cauline internodes, reportedly white petals, basally cuneate, glabrous leaves, and broadly campanulate hypanthia crowned by rounded, deltoid sepals. I have tentatively assigned this collection to the typical subspecies. Additional material with mature capsules and seeds, however, may necessitate a reappraisal of its taxonomic status. Although variants of this subspecies often differ strikingly in appearance, it seems evident from the constancy of such unifying characters as the flowers, hypanthia, and seeds that we are dealing with many localized expressions of a polymorphic taxon.

4b. **Centradenia grandifolia** (Schlechtd.) Endl. subsp. **brevisepala** (Gleason) Almeda, comb. nov. FIGURE 9F.

Centradenia grandifolia var. *brevisepala* Gleason, Phytologia **1**: 340. 1939. TYPE: Guatemala. Alta Verapaz: along trail to Rubel Cruz cave, 3–4 km. w. of Finca Pansamala, *Stuart 15* (holotype: MICH!).

Mature hypanthia campanulate, broadest distally at the torus, 6–7 mm. long, glabrous, not at all accrescent or bladdery, but closely enveloping the obovoid ovary. Sepals depressed-ovate, apically truncate to mucronulate, 1–2 mm. long. Petals white. Pollen 12.5–13.7 μm. in diameter. Seeds ± dolabriform, muricate or with low, dome-shaped processes.

Flowering: December to April.

DISTRIBUTION. Known only from a few scattered localities in Alta Verapaz, Guatemala. Reportedly collected at an elevation of 3800 feet.

REPRESENTATIVE SPECIMENS. **Guatemala.** ALTA VERAPAZ: Pansamala, *Donnell Smith 1540* (US); trail to Senahú, *Goll 168* (US); vicinity of Pansamala, *von Tuerckheim 883* (US); finca Trece Aguas, *Wilson 184* (F).

This rarely collected, presumably localized subspecies is known from only five collections, the most recent gathered in 1939. During a recent visit to the type locality and surrounding areas, I was unable to locate any populations of this taxon. It would be premature, however, to suggest that it is rare or on the verge of extinction, for many areas of Alta Verapaz await thorough botanical exploration.

A case could be made for recognizing this taxon at the specific level. Unlike Williams (1963), I have chosen not to adopt this course of action for I feel that it would misrepresent our current knowledge of this entity and obscure its overriding floral and vegetative similarities to the typical subspecies.

UNCERTAIN SPECIES

Centradenia ovata Kl. in Otto & Dietr. Allg. Gartenz. **19**: 354. 1851. TYPE: Central America, without further locality, *Warscewicz s.n.* (holotype: presumably at B and destroyed).

The generalized original description coupled with the lack of authentic material prohibit unequivocal disposition of this epithet. In the treatment of *Centradenia* by Klotzsch, *C. ovata* was the only constituent of a presumed section (*Homalophyllum*) characterized by subequal, persistent, basally more or less symmetric leaves. This, together with the protologue description of the inflorescence as ". . . cymis terminalibus trichotomis . . . ," suggests that this species may be synonymous with *C. floribunda*. Unfortunately, the imprecise collection locality and the absence of a description of the stamens preclude assignment of *C. ovata* to either of the two subspecies of *C. floribunda* recognized in this treatment.

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COMPARATIVE ANATOMY AND SYSTEMATICS OF MOUTABEAE (POLYGALACEAE)*

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THE POLYGALACEAE, as now generally constituted, contain three tribes: Polygaleae, Xanthophylleae, and Moutabeae (van Royen & van Steenis, 1952; Scholz, 1964; Hutchinson, 1967). However, their generic constitution and ordinal position have proven problematical. The genera which have been shifted in and out of the family most frequently are *Xanthophyllum* Roxb. (Wettstein, 1935; Dube, 1962; Cronquist, 1968) and *Diclidanthera* Mart. (Miers, 1861; Gürke, 1891; Chodat, 1896; Perkins, 1907; Gilg, 1908; Engler & Gilg, 1924; Sprague, 1940; O'Donell, 1941; Pittier, 1942; Erdtman, 1944; Metcalfe & Chalk, 1950). In addition, the affinities of *Barnhartia* Gleason (Gleason, 1926) and *Moutabea* Aublet (Endlicher, 1839) have not been clear. This study of the vegetative anatomy of members of the tribe Moutabeae was undertaken to clarify the relationships of the taxa of this group.

DESCRIPTIONS AND DISTRIBUTIONS

Polygalaceae tribe **Moutabeae** Chodat (1896). Shrubs, lianas, or trees. Leaves alternate, simple, entire. Calyx and corolla united at the base (a feature which separates the Moutabeae from the other tribes of the Polygalaceae), calyx gamosepalous, corolla polypetalous to gamopetalous. Stamens 7, 8, or 10, monadelphous or subdiadelphous, or free and adnate to free petals; anthers dehiscing by a slit. Ovary syncarpous, 2–8-locular, with 1 ovule per locule. Three genera with ca. 19 species in South America and Panama; one monotypic genus in New Guinea and the Solomon Islands (van Royen & van Steenis, 1952; Hutchinson, 1967).

1. **Barnhartia** Gleason (1926). Liana growing to the tops of trees. Inflorescence a leafy, axillary or terminal panicle; flowers subzygomorphic; sepals and petals 5; petals connivent, not fused, with orange claws and maroon blades; stamens 7–8, adnate to petals; ovary 2- or 3-locular; apex of petiole with glands. One species, *B. floribunda*. Guyana, Surinam, Brazil, and Venezuela.

2. **Diclidanthera** Martius (1827). Small trees or lianas. Inflorescence a terminal or axillary raceme or panicle; calyx 5-lobed; corolla tube 5-lobed and white; stamens 8 or 10, monadelphous; anthers glabrous; ovary 5-locular. About 8 species. Brazil, Venezuela, Colombia, and Peru.

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3. **Eriandra** van Royen & van Steenis (1952). Tree to 80 feet. Inflorescence a small, few-flowered axillary raceme; flowers white, scented; sepals 4–5; petals 4–5, free at apex only; stamens 8 or 10, monadelphous; anthers densely pubescent; ovary 7–8-locular. One species, *E. fragrans*. Solomon Islands and New Guinea.

4. **Moutabea** Aublet (1775). Tree to 35 feet, shrubs or lianas. Inflorescence a short axillary raceme; flowers strongly zygomorphic; sepals and petals 5; corolla tubular; stamens 7 or 8, diadelphous; ovary 4–5-locular; seed without endosperm. About 10 species. Brazil, French Guiana, Guyana, Venezuela, Colombia, Peru, and Panama.

TAXONOMIC HISTORY

Moutabea was described by Aublet in 1775 and was placed among the Monadelphia, Pentandria. Endlicher (1839) listed *Moutabea* among the *genera dubiae affinitatis* at the end of his ordo Ebenaceae, while Lindley (1846) placed it in the Polygalaceae. Miquel (1856) treated *Moutabea* as a member of the Ebenaceae, although in his discussion of its placement, he suggested that it belonged in the Polygalaceae. For the most part, Lindley's placement of *Moutabea* in the Polygalaceae has been followed to the present day. Chodat (1896) established the tribe Moutabeae in which he included only *Moutabea*.

Diclidanthera was named and described by Martius in 1827, and was placed in the Ebenaceae. Reichenbach (1828) listed *Diclidanthera* among the Styraceae which, in turn, were listed under the family Sapotaceae. Reichenbach's placement of *Diclidanthera* among the Styraceae was accepted by many botanists. It is interesting that Reichenbach also included *Moutabea* in the Sapotaceae; therefore, almost immediately after the description of *Diclidanthera* it was tenously linked with *Moutabea*. Lindley (1836) listed *Diclidanthera* under his Styraceae, which he tentatively positioned as a suborder of the Ebenaceae. Endlicher's (1839) disposition of the genus was similar. More recently, Bentham (1876) and Gürke (1891) also included *Diclidanthera* in the Styracaceae.

Other authors disagreed with the treatments noted above. De Candolle (1844) enumerated several ways in which *Diclidanthera* differed from both the Styracaceae and the Ebenaceae. Perkins removed *Diclidanthera* from the Styracaceae in 1907, and although she had no suggestions for its proper position, it was not again treated as a member of that family. Gilg (1908) agreed with Perkins and assigned *Diclidanthera* to its own family, the Diclidantheraceae; this usage has been followed by some until recently (Wettstein, 1935; Engler & Diels, 1936; Metcalfe & Chalk, 1950). Gilg, however, had been anticipated by Agardh, who published the Diclidantheraceae in 1858. Thus, Diclidantheraceae Gilg is a later homonym of Diclidantheraceae Agardh. Miers (1861) first thought *Diclidanthera* was hamamelidaceous but later changed his mind and placed it in the Byttneriaceae. He wrote that ". . . *Diclidanthera* bears little relation toward the

Ebenaceae, Styraceae or Polygalaceae . . . ," indicating that some botanists had found a place for *Diclidanthera* in the Polygalaceae, as Miquel (1856) and Martius (von Mohl & von Schlechtendal, 1856) had indeed suggested.

Miquel's and Martius's belief that *Diclidanthera* should be placed in the Polygalaceae was greatly strengthened by two quite unrelated events. First, Gleason (1926) described a new genus, *Barnhartia*, which was soon shown (Sprague & Sandwith, 1932; Sprague, 1940) to be intermediate in floral structure between *Diclidanthera* and *Polygala*, thus linking *Diclidanthera* to the Polygalaceae. The second important occurrence was associated with botanists' growing awareness of the necessity to study as many characters as possible when determining the affinities of troublesome plants. In this case, *Diclidanthera* pollen was shown to be ". . . of a type peculiar to the Polygalaceae . . ." (Sprague, 1940), a fact confirmed by Erdtman (1944, 1952). Once *Diclidanthera* was shown to be a member of the Polygalaceae, the fusion of its sepals and petals into a tube made its affinity to *Moutabea* and its placement in the tribe Moutabeae obvious. The position of *Diclidanthera* in the Moutabeae is supported by the observation that all Moutabeae (*Moutabea*, *Diclidanthera*, *Barnhartia*, and *Eriandra*) appear to be aluminum accumulators (Chenery, 1948; van Royen & van Steenis, 1952; Hegnauer, 1969).

It is interesting to note, despite the various treatments of *Diclidanthera* and *Moutabea*, that ever since Reichenbach first indicated an affinity between them, these two genera have often been placed near each other in taxonomic studies (Lindley, 1836; Endlicher, 1839; Miquel, 1856; von Mohl & von Schlechtendal, 1856; De Candolle, 1873). However, it was not until the discovery of *Barnhartia* that this affinity was clarified.

Gleason described *Barnhartia* in 1926. He thought that its floral structure indicated a relationship with the Styracaceae, but also noted a likeness to *Diclidanthera*. He commented that Perkins had excluded *Diclidanthera* from the Styracaceae, thus leaving the position of his new genus in question. As mentioned above, Sprague and Sandwith (1932) saw the importance of *Barnhartia* as a link between *Polygala* and *Diclidanthera*. Thus, *Barnhartia*, *Diclidanthera*, and *Moutabea* (which Martius had suggested was closely related to *Diclidanthera*) all came to be associated in the Moutabeae.

The last genus to be placed in the Moutabeae was *Eriandra*, described by van Royen and van Steenis in 1952. Although *Eriandra* was from New Guinea and not South America (as were other members of the tribe), thus creating what the authors considered a "most remarkable" distribution, van Royen and van Steenis were convinced *Eriandra* was ". . . closely related to *Diclidanthera*, *Moutabea*, and *Barnhartia*."

Members of the Moutabeae are of little economic importance. Record and Hess (1943) list *Moutabea* in their *Timbers of the New World*, but give no uses, mentioning only that it is a climber. However, several common names (graine macaque, aymoutabou, caimito do monte, gogo de guariba, graõs de macaco) exist for *Moutabea*, indicating local familiarity and per-

haps some economic importance (Aublet, 1775; Oort, 1939; Record & Hess, 1943). *Moutabea* fruit is said to be edible (Macbride, 1950; Lewis & Herrera-MacBryde, 1969). A herbarium label (*Forest Department of British Guiana 3015*) states that the stem of *Barnhartia* makes "a strong rope used for stringing timbers from ballahoos [schooners with the foremast raking forward and the mainmast aft]."

ANATOMICAL REVIEW

Metcalfe and Chalk (1950) stated that "the anatomy of the Brazilian shrubs and trees belonging to the genus *Diclidanthera* is rather imperfectly known." The same may be said for the other three genera of Moutabeae. Only passing references to anatomical information are available for *Eriandra* (van Royen and van Steenis, 1952) and *Barnhartia* (Metcalfe & Chalk, 1950; Sprague, 1940).

In their summary of the anatomy of *Diclidanthera*, Metcalfe and Chalk (1950) noted that the dorsiventral leaf has hairs divided by thin septa, a hypoderm of 1 to 2 layers below the upper epidermis, and a palisade layer about 3 cells thick. Veins are sheathed by thick-walled fibers, and numerous crystals occur in cells adjacent to these fibers. Based on O'Donell (1941), their description of the wood noted mostly solitary vessels with simple perforations and alternate intervascular pitting, vasicentric parenchyma, heterogeneous rays of types IIA and IIB (Kribs, 1935), and fibers with large bordered pits. Metcalfe and Chalk also mentioned anomalous secondary thickening in the stem. Solereder (1908), Gürke (1891), and Erdtman (1944) have also made contributions to the anatomical studies of *Diclidanthera.*

The anatomy of *Moutabea* has probably received more attention than that of any other member of the tribe. Unfortunately, most of this work has been in conjunction with broad surveys which did not include detailed generic descriptions, although specific details were occasionally noted. For instance, Metcalfe and Chalk (1950) included *Moutabea* in their treatment of the Polygalaceae and only the following facts can be applied with certainty to *Moutabea* leaves: they are dorsiventral; the epidermal cells have straight anticlinal walls; a hypoderm and long sclerosed cells in the palisade layer are present in *M. guianensis*; the midrib is two-stranded, the upper strand of which is inverted. A small amount of additional information is available on *Moutabea* in Erdtman (1944) and Foster (1947). More information is available on the wood anatomy of *Moutabea* than on the leaf anatomy. Wood anatomy may be summarized as follows: pores are solitary, scattered, large or occasionally small; tyloses may be present; intervascular pits are medium to coarse; vessel to ray pit-pairs are half-bordered; rays are heterogeneous (Kribs Type IIA, 1935) and 6–8 cells wide; axial xylem parenchyma is diffuse-in-aggregates and scanty paratracheal (Metcalfe & Chalk, 1950; Record & Hess, 1943; Biswas, 1969; Heimsch, 1942).

Although several papers have dealt with anomalous growth in polygala-

ceous lianas (Crüger, 1850; Müller, 1866; Schenck, 1893; Pfeiffer, 1925, 1926), these have usually given descriptions and illustrations of genera in the Polygaleae, mainly *Securidaca*. Chodat (1896) described anomalous growth in *Moutabea* as being formed by half-moon- or sickle-shaped segments of xylem which are added onto the central cylinder. Pfeiffer (1926) wrote that anomalous growth in *Moutabea* is of the concentric stem type (*corpus lignosum circumvallatum*). Meristematic action which forms this type of anomaly was attributed by Chalk and Chattaway (1937) to a short-lived cambium, replaced periodically by new meristematic tissue originating either in the pericycle or the cortex which repeats the structure of the young stem. De Bary (1884), however, believed that new cambia originated in the "bast-zone."

MATERIALS AND METHODS

Specimens studied in this investigation are documented in TABLE 1. With the exception of several prepared slides obtained from Jodrell Laboratory, Royal Botanic Gardens, Kew, and fluid-preserved leaves and wood of *Moutabea guianensis* Aublet, all specimens were dried, either leaves from herbarium sheets or dried wood samples.

Standard techniques were used in preparing these materials for study. The dry wood samples were boiled in an "Aerosol OT" solution in a reflux apparatus for periods of up to four days in order to rehydrate and soften the wood. (This procedure is a modification by Rock (1972) of a technique outlined by Ayensu (1967).) Fluid-preserved wood was not treated in this way prior to embedding. Following embedding in celloidin, the material was stored in a 1:1 solution of glycerin and 95% ethanol. Transverse, radial, and tangential sections were cut on a sliding microtome, stained in Heidenhain's iron-alum haematoxylin, counter-stained with safranin, dehydrated, and mounted in Canada balsam.

Macerations were prepared following a variation of Jeffrey's method (Rock, 1972).

Dry leaves were boiled briefly in water to rehydrate them. Fluid-preserved leaves were not so treated. Clearings were prepared using a modification of Arnott's (1959) technique. Leaves were first treated with 5% NaOH, washed in water, immersed in Stockwell's solution (Johansen, 1940), washed in water again, then immersed in chloral hydrate. After a final washing, the leaves were stained in safranin, dehydrated, and mounted in Canada balsam. Because the large number of sclereids in some species of *Moutabea* rendered the clearing process ineffective, additional preparations of some of this material were prepared in the following manner: after the final wash of the clearing process, the lower epidermis was stripped away, stained in safranin, dehydrated, and mounted in Harleco Synthetic Resin (HSR). The sclereids were then scraped off the remaining piece of leaf, stained in safranin, dehydrated, and mounted in HSR.

Transverse and paradermal sections of leaves were prepared from material embedded in paraffin. Sections were cut at 10 micrometers (μm.) on

TABLE 1. Specimens of Moutabeae examined.

SPECIES [1]	COLLECTOR [2]	COLLECTION LOCALITY	HERBARIUM [3]	XYLARIUM [4]	LEAF	WOOD	SLIDES [5]
Barnhartia floribunda Gleason	Boschwezen 6707	Surinam	U		+		
	L.B.B./Boerboom 8732	Surinam	BBS		+		
	de la Cruz 2727	British Guiana	NY		+		
	Sandwith 507	British Guiana	NY	K–JW			l, t
Diclidanthera bolivarensis Pittier	Wurdack & Monachino 41332	Venezuela	US		+		
Diclidanthera elliptica Miers	Hoehne 28421	Brazil	NY, US		+		
Diclidanthera laurifolia Martius	Mexia 5141	Brazil	NY, US	K–JW	+		l, t
	Riedel 1158	Brazil	U, NY		+		
Diclidanthera octandra Gleason	Froés 24037	Brazil	US		+		
Diclidanthera penduliflora Martius	Murça Pires & Black 1727a	Brazil	US		+		
	Spruce 1030			K–JW			l, t
Eriandra fragrans van Royen & van Steenis	Boschwezen 5810	West Irian, New Guinea		FPAW		+	
	C. Koster (Boschwezen 8062)	West Irian, New Guinea	FPA, L	FPAW	+	+	
Eriandra fragrans van Royen & van Steenis	Boschwezen 11903	New Guinea	L	LW		+	
	Pullen 1151	New Guinea	L	FPAW	+	+	
	F. C. Whitmore (British Solomon Islands Protectorate 1413)	Solomon Islands	L		+		
Moutabea aculeata (Ruiz & Pavon) Poeppig & Endlicher	Klug 3936	Peru	US, NY		+		
Moutabea excoriata Martius ex Miquel	Smith 4674	Brazil	US		+		
Moutabea guianensis Aublet	Pulle 389	Surinam	L, U	UW 6498	+	+	
	Murça Pires *s.n.*	Brazil	T [6]		+ [7]	+ [7]	
	Van Donselaar 3193	Surinam	U	UW 12022	+	+	
Moutabea longifolia Poeppig & Endlicher	Krukoff 7056	Brazil	US, NY	AW 37053, PRFW		+	
	Froés 11709	Brazil	NY		+		
Moutabea sp.	Wurdack & Adderly 43409	Brazil	US	USW 17988	+	+	

[1] Names used are those originally associated with specimens.
[2] If the collector is unknown or if he did not number the specimen, the collection is identified by an institutional number.
[3] Herbarium abbreviations follow those recommended by Holmgren and Keuken (1974) in *Index Herbariorum*, ed. 6.
[4] Xylarium abbreviations follow those recommended by Stern (1967) in *Index Xylariorum*.
[5] Prepared microscope slides from K–JW: l = leaf section; t = twig section.
[6] Murça Pires writes of this material: "It is the same species which has been collected by Archer [i.e., William Andrew Archer] and is represented at the U. S. National Herbarium (US): *Archer 7978, 8252, 8215, 7904.*"
[7] These represent the only fluid-preserved materials; all other materials were dried.

a rotary microtome, stained with Heidenhain's iron-alum haematoxylin and safranin, and mounted in HSR. Since the staining technique employed often dissolved out any crystals present (Stern *et al.*, 1970), one slide of each specimen was mounted unstained.

Diagnostic characters used in describing the woods were selected from those suggested by Tippo (1941) and Tamolang *et al.* (1963). Except for *Barnhartia* and *Diclidanthera*, where measurements were made from sections because the small bits of stem available precluded maceration, lengths of imperforate tracheary elements and vessel elements were measured from macerated material. Pore distribution, pore diameter, and vessel element end wall angle were measured from sectioned material. The total tip-to-tip length of vessel elements was recorded. Since ligules often are not visible in section, measurements of vessel element length made from sections probably resulted in lengths shorter than the true values. Tangential pore diameters were measured from middle lamella to middle lamella. End wall angles were measured in degrees with a goniometer eyepiece. Pore distribution was determined by counting the numbers of solitary pores, pore clusters, and radial pore multiples from ten random fields of view. The percentage of pore groupings for each class was computed by dividing the frequency for each class by the total frequency for all classes.

Photographs were prepared in two ways. Some were prepared by conventional photomicrography using an attachment camera on a Wild M-20 compound microscope. Other photographs were made by placing the specimen-containing microscope slide itself on the stage of a photographic enlarger and projecting an image of the specimen directly onto photographic paper; that is, the mounted specimen was used instead of a photographic negative. Magnifications of up to 16× were possible with a 50 mm. enlarging lens. A print made in this way has a negative image (FIGURES 1–5). The positive print seen in FIGURE 11 was obtained by making a contact print of the original negative print.

Diagnostic characters to be used in describing leaves were selected from Esau (1965) and developed through discussion with W. L. Stern. Length and diameter of stomatal apparatuses were measured either from clearings or from paradermal sections; cuticle thickness was measured from transverse sections.

Measurements were rounded according to the following schedule: 0–10 μm. to the nearest 0.1 μm., 11–100 μm. to the nearest 1 μm., above 100 μm. to the nearest 10 μm.

Terminology used in the description of woods follows that of Tamolang *et al.* (1963) and is largely in accord with that of the Committee on Nomenclature, the International Association of Wood Anatomists, *International Glossary of Terms Used in Wood Anatomy* (1957), except for the description of axial xylem parenchyma which follows Hess (1950). Hess's categories of axial xylem parenchyma seemed more suited to the situation in Moutabeae than did those of other systems.

One arrangement of axial parenchyma found in Moutabeae is not in-

cluded in any of the usual groupings. This arrangement here termed "paratracheal diffuse with wings," resembles aliform parenchyma, but cannot be included in that category since the parenchyma does not completely surround the vessels. Furthermore, the wings are not solid parenchyma, but have imperforate tracheary elements scattered through them (FIGURE 9).

Bailey (1936) stressed the likelihood of finding genera with transitional series of cells between tracheids and fiber-tracheids, or between fiber-tracheids and libriform wood fibers. The former transition is present in Moutabeae, where imperforate tracheary elements vary from thin-walled, blunt-ended tracheids with pits of the same magnitude as intervascular pits, to thicker-walled, tapered fiber-tracheids with small bordered pits. The distinction between tracheid and fiber-tracheid is particularly hard to define in the Moutabeae because the vessel elements, and consequently the intervascular pits, vary greatly in size, making comparisons of pit borders difficult.

Growth rings which encircle the whole stem are absent in Moutabeae. However, faint, partial rings spanning short arcs are present and are termed "growth arcs." The ground mass of xylem, excluding conjunctive parenchyma and included phloem, is for convenience termed "normal xylem." The term "pithlike" is strictly descriptive and implies nothing about the origin or function of the tissue.

Terminology of leaf anatomy follows Esau (1965); terms for leaf architecture are based on Hickey (1973). Application of the terms "biseriate," "triseriate," or "multiseriate" to leaf epidermal structure is purely descriptive and does not imply ontogenetic derivation.

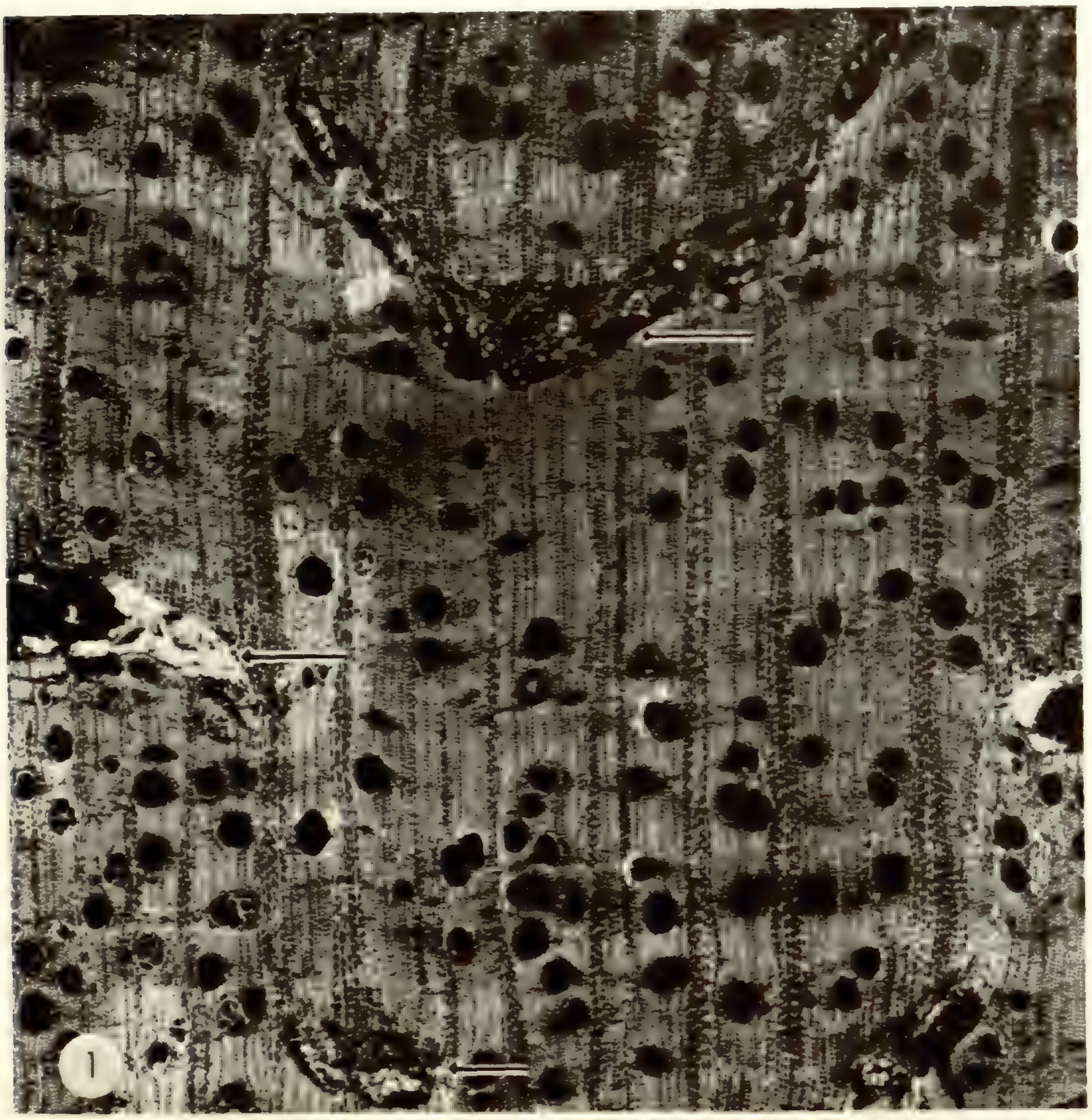
In citing literature, when the date of actual publication is different from that found on the title page of a book, that given in Stafleu's *Taxonomic Literature* (1967) has been accepted.

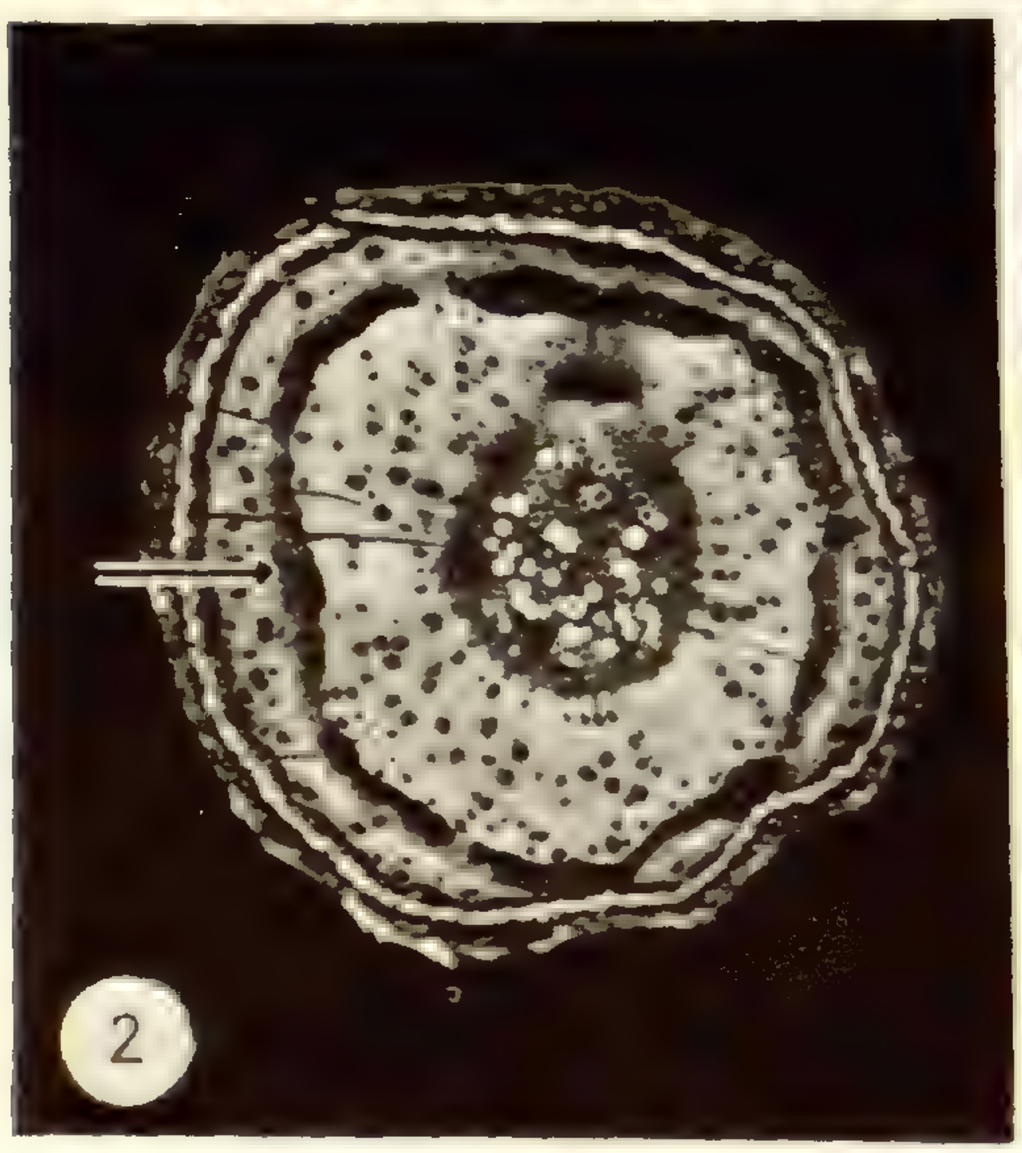
ANATOMY

Barnhartia floribunda

WOOD. Wood for study of this genus was unsatisfactory because twigs taken from herbarium specimens do not show mature structure. However, comparison with similar material of other genera in the Moutabeae gives some insight into similarities and differences among these genera.

Growth arcs are absent. Pores are of fairly uniform size throughout the wood (FIGURE 3). Distribution of pore groups is 97.4% solitary and 2.6% radial multiples. Pore outline is circular or slightly angular in some of the narrower vessels. Vessel wall thickness varies from 1.4 to 2.7 μm. Tangential pore diameter averages 48 μm., with a range of 20 to 82 μm. Perforation plates are exclusively simple, generally with round perforations having only a very slight border. Tyloses are absent. Vessel element length (measured from sections) averages 410 μm., with a range of 160 to 580 μm. Intervascular pitting is alternate and pits are circular-bordered. Diameter of the pit border ranges from 6.8 to 8.1 μm. Inner





FIGURES 1–3: 1, *Eriandra fragrans*, transverse section of stem showing distribution of included phloem (arrows), × 12; 2, *Diclidanthera laurifolia*, transverse section of young stem showing first arc of included phloem (arrow), × 12; 3, *Barnhartia floribunda*, transverse section of young stem, × 12.

apertures are slitlike and crossed. Vessel element end wall angle ranges from 25° to 80°. Imperforate tracheary elements range from tracheids to fiber-tracheids. The pits are similar in shape to intervascular pits. Wall thickness ranges from 2.0 to 5.4 μm.

Vascular rays are both homocellular and heterocellular. Homocellular rays are nearly all uniseriate, ranging from 3.4 to 8.5 μm. wide and from 2 to 12 cells (54 to 450 μm.) high. All cells are erect. Heterocellular rays are mostly uniseriate and biseriate, but a few triseriate rays occur. Ray width varies from 8.5 to 24 μm., and height from 9 to 126 cells (220 to 3440 μm.). Cells of heterocellular rays range from procumbent to square or short erect cells, with tall erect cells forming uniseriate wings. Vessel to ray parenchyma pitting is half-bordered, the vessel side of the pit-pair having a circular border and a slitlike inner aperture, the ray side a simple pit corresponding to the border on the vessel side. No crystals or deposits occur in the ray parenchyma. Sheath cells are absent.

Axial xylem parenchyma is not abundant. A small amount of diffuse parenchyma is present, as well as some tangential parenchyma. Paratracheal diffuse parenchyma is also present. Vessel to axial xylem parenchyma pitting resembles vessel to ray pitting, i.e., pit-pairs are half-bordered with the circular border and slitlike inner aperture on the vessel side.

INCLUDED PHLOEM. No included phloem was observed (FIGURE 3).

LEAVES. *Barnhartia* leaves are simple and unlobed, with entire margins. Venation is pinnate; more specifically, brochidodromous. Areolation is mostly well developed and is partially oriented (see Hickey, 1973, for definition of terms). Veinlets are simple or branched, have clavate endings, and are not recurved. They consist of large, thin-walled, spirally thickened elements (probably tracheids) and are entirely surrounded by thin-walled bundle sheath cells.

Surfaces of *Barnhartia* leaves are more or less flat, and there are no unusual or pronounced topographic features.

Leaves are dorsiventral. The palisade layer usually consists of one full, complete layer, plus a second layer which is incomplete, considerable space occurring between adjacent palisade cells of the second layer. Sometimes a partial third layer is observed. One of the four samples studied differs considerably from this description. Sections of *Sandwith 507* possess a complete second palisade layer in which the cells are closely placed. Even the incomplete third layer is fairly extensive; the differences are heightened by the greater length of the palisade cells in the Sandwith collection than that observed in the other collections. Cells of the lower layer of the palisade in all collections are transitional with those of the subadjacent spongy layer. The configuration of the spongy mesophyll is modified slightly from the usual lacunose type because the branching of cells seems to be largely in the same plane as that of the blade, with few branches extending perpendicularly to this plane. This arrangement is most pronounced toward the abaxial side of the leaf.

Rhomboid and polyhedral crystals occur in abundance in the outermost

layer of bundle sheath cells. A small number of crystals occurs in the palisade cells next to the hypodermis and in the spongy cells next to the abaxial epidermis.

Except for the primary vein, vascular bundles of the leaves in *Barnhartia* consist of a single collateral bundle. The primary vein (as seen in transverse section) is more complex, consisting of a large area of xylem with phloem in round to oblong patches abaxial to it (FIGURE 12). In addition, there are one or two smaller areas of xylem adaxial to the large area of xylem and separated from it by a pithlike central region of parenchyma. This parenchyma is broken down in varying degrees, leaving small to large cavities next to the xylem (FIGURE 12, arrow). Possibly these cavities formed while the leaves were drying and are artifacts. The one or two smaller areas of xylem are flanked on their adaxial side by a variable thickness of phloem. Terminal veinlets lack phloem.

All veins except the terminal veinlets have a sheath of sclerenchyma between the vascular tissue and the bundle sheath. This sclerenchyma is widest in the primary vein and decreases in width with decreasing size of the vein; the smallest veinlets lack sclerenchyma altogether.

Bundle sheath cells are thickened on their radial and inner tangential walls, giving the bundle sheath the appearance very often seen in endodermides. Thickening of bundle sheath cells disappears in the smaller veins with the disappearance of the sclerenchyma sheath. The bundle sheath forms a continuous covering from the terminal veinlets to the primary vein. Bundle sheath extensions are absent.

The lower epidermis is uniseriate; the upper epidermis is largely triseriate. However, the number of epidermal layers over the primary vein may be as many as five, while in other areas of the blade the innermost epidermal layer is replaced by palisade cells.

In face view, the epidermal cells of both leaf surfaces are polygonal. The outer layer of the adaxial epidermis differs from the two inner layers in having smaller and mostly paired cells. Each pair is surrounded by a common, relatively thick cell wall, but is divided by a thin septum.

In sectional view, epidermal cells are square to rectangular. The cuticle is smooth-surfaced, varying in thickness from about 3 to 7 μm.

Stomata are restricted to the lower epidermis, where they are evenly distributed over the surface. The stomatal apparatus is anomocytic, no accessory cells being distinguishable. Guard cells are reniform; the pair roughly circular (length/width = 0.99). Guard cells are provided with a prominent outer cuticular ridge which projects beyond the surface of the leaf, as well as an inconspicuous inner ridge. In a median cross section of the guard cells, the periclinal walls are very heavily thickened, while the anticlinal walls are thin. No trichomes or hydathodes were observed.

Diclidanthera

WOOD. *Diclidanthera* wood was observed from slides prepared at the Jodrell Laboratory, Royal Botanic Gardens, Kew. These slides, prepared

from herbarium material, do not include mature wood. Only two species, *D. laurifolia* and *D. penduliflora*, were studied. Stems of the latter were represented only by transverse sections. Thus, pore distribution, pore diameter, pore outline, vessel wall thickness, and axial xylem parenchyma distribution represent the only combined data, since data requiring longitudinal sections could not be obtained for *D. penduliflora*.

Growth arcs, absent in *D. penduliflora*, are present in *D. laurifolia* (FIGURE 2). Pores are of uniform size distribution throughout. Distribution of pore groups is 88.7% solitary, 9.7% clusters, and 1.6% radial multiples in *D. penduliflora*; 98.1% solitary and 1.9% clusters in *D. laurifolia*. Pore outline is circular, with a slight angularity occurring in the narrower vessels. Vessel wall thickness varies from 2.0 to 4.1 μm. Tangential pore diameter averages 46 μm., with a range of 14 to 85 μm. Perforation plates are exclusively simple with essentially round perforations. Perforations have no (or only vestigial) borders. Tyloses are absent. Vessel element length (observed only in section) averaged 380 μm. and ranged from 210 to 580 μm. Intervascular pitting is alternate and circular-bordered. Pit-border diameter ranges from 5.4 to 6.8 μm. Inner apertures are slitlike and one half to three fourths the width of the border. End wall angle ranges from 10° to 89°. Imperforate tracheary elements range from tracheids to fiber-tracheids. Pits are the same shape as the intervascular pits. However, in elements most resembling fiber-tracheids, pits have longer inner apertures than do the intervascular pits. The longer inner apertures are positioned almost vertically in contrast to the almost horizontal apertures in the intervascular pitting. Wall thickness of imperforate tracheary elements ranges from 2.0 to 5.4 μm.

Vascular rays are both homocellular and heterocellular. Homocellular rays are mostly uniseriate, from 3.4 to 10.2 μm. wide, and consist of erect cells. Homocellular rays vary in height from 1 to 51 cells (48 to 1920 μm.). Heterocellular rays are usually uniseriate or biseriate. Ray width varies from 6.8 to 17 μm., and height from 3 to 53 cells (110 to 1950 μm.). The heterocellular rays consist of tall erect, square, and short procumbent cells. The tall erect cells often form uniseriate wings. Vessel to ray parenchyma pitting is half-bordered. Pits in vessel element walls have circular borders and slitlike inner apertures; those in ray cell walls are simple and coincide with the shape of the pit border in vessel element walls. No crystals or deposits occur in the ray parenchyma. Sheath cells are absent.

Axial xylem parenchyma is sparse; that which occurs is diffuse paratracheal. Vessel to axial parenchyma pitting resembles vessel to ray pitting. No crystals or deposits were observed.

INCLUDED PHLOEM. Included phloem occurs in the specimen of *D. laurifolia*, but not in that of *D. penduliflora*, possibly because of its immaturity. I suspect that older material would reveal the presence of included phloem in *D. penduliflora*. The included phloem of *D. laurifolia* contains sclereids, fibers, sieve tube elements, and axial parenchyma cells which contain crys-

FIGURE 4: *Eriandra fragrans*, radial section of stem, × 12.

tals. The arrangement of included phloem in *D. laurifolia* is shown in FIGURE 2.

LEAVES. *Diclidanthera* leaves are simple and unlobed; margins are entire (FIGURE 11). Venation is brochidodromous. Areolation is mostly well developed and is partially oriented. The simple or branched veinlets have moderately clavate endings which are not recurved. Veinlets consist of thin-walled, spirally thickened tracheary elements (probably tracheids) up to five times as wide as those found in the larger veins. Since the length of these enlarged elements remains constant, the resulting cells are roughly spherical. Thin-walled bundle sheath cells completely enclose the veinlets.

Surfaces of *Diclidanthera* leaves are nearly plane. Leaves are dorsiventral. Most species examined have a biseriate palisade layer with some triseriate regions. *Diclidanthera octandra* has a uniseriate palisade layer with some biseriate regions; *D. laurifolia* and *D. penduliflora* may have small uniseriate regions in an otherwise biseriate palisade. It is difficult to draw firm conclusions concerning the shape of the palisade cells because of the poor preservation of some of the material. In some of the species (*D. elliptica*, *D. laurifolia*, *D. octandra*, and *D. penduliflora*), the palisade cells appear very squat, sometimes almost square. I suspect that this is related to the manner in which leaves were pressed and dried, for one specimen of *D. penduliflora* displays typical, vertically elongated palisade cells. *Diclidanthera bolivarensis* also displays typical palisade cells, except for a few cells which are divided periclinally in the middle, yielding squat, almost square cells. The boundary between the palisade and spongy layers is often indistinct. Spongy mesophyll is of the typical lacunose type, with some compaction next to the abaxial epidermis. Spongy mesophyll cells having the same horizontal aspect noted in *Barnhartia* occur in *D. elliptica*, *D. laurifolia*, and *D. octandra*, but to a lesser degree. This feature may also be related to the pressing of leaves when they were prepared as herbarium specimens.

Rhomboid and polyhedral crystals are common in the bundle sheath cells of *Diclidanthera*. In addition, other crystalline forms occur in these cells in *D. bolivarensis* and *D. laurifolia*. The former species has very small, lenticular crystals, and two crystals sometimes intersect one another in some of the palisade cells. The latter species has groups of small druses in cells of the upper palisade and, to a lesser degree, in cells of the lowest portion of the spongy mesophyll.

All veins except the primary vein have a single collateral bundle. The primary vein is more complex and is dominated by a large arc of xylem on the abaxial side of the vein. This xylem arc is flanked by phloem on its abaxial side. In transverse section, a smaller area of xylem occurs on the adaxial side of the bundle. The smaller xylem area is flanked by phloem on its adaxial side. Between the two areas of xylem is a pithlike region of parenchyma, some of which breaks down to yield lacunae adjacent to the abaxial xylem. The terminal veinlets lack phloem.

The primary vein has a thick sheath of sclerenchyma between the vascular tissue and the bundle sheath. The smaller veins also have sclerenchyma sheaths. The width of the sheath decreases with decreasing vein size; the terminal veinlets lack sclerenchyma altogether.

A bundle sheath covers the entire vein system from primary vein to terminal veinlets. In larger veins, bundle sheath cells are thickened on their radial and inner tangential walls. Coincident with the decrease in the sclerenchyma sheath is a decrease in the thickening of the bundle sheath cells until, in the terminal veinlets, the bundle sheath cells have no secondary thickening at all. Bundle sheath extensions are absent.

The lower epidermis in *Diclidanthera* is uniseriate. The upper epidermis is triseriate over the primary vein and biseriate elsewhere, except in *D. bolivarensis*, where it is mostly triseriate with some biseriate patches. *Diclidanthera laurifolia* has some triseriate patches other than those over the primary vein.

In face view, leaf epidermal cells are polygonal. All species have pairs of cells in the epidermis which are similar to those in *Barnhartia* (FIGURE 13). In *D. bolivarensis*, *D. elliptica*, and *D. laurifolia* numerous epidermal cells are paired, whereas in *D. octandra* and *D. penduliflora* only a few paired cells occur.

In sectional view, epidermal cells are generally rectangular, although some square cells are seen. The cuticle is smooth-surfaced and varies in thickness from 1 to 4 μm.

Stomata are restricted to the lower epidermis, where they occur randomly over the surface. The stomatal apparatus is anomocytic (FIGURE 13). Guard cells are reniform; a pair nearly circular (length/width = 1.01). The guard cells have a prominent outer cuticular ridge which extends beyond the surface of the leaf, as well as an inconspicuous inner ridge. In median cross section, the guard cells have thickened periclinal walls and thin anticlinal walls.

Neither collection of *D. laurifolia* has trichomes; both collections of *D. penduliflora* have hairs, as do *D. elliptica* and *D. octandra*. Trichomes are heavily cuticularized and consist of uniseriate hairs divided into several cells by thin septa. Trichomes occur on both sides of the leaf and may be plentiful (*D. elliptica*) or very sparse (*D. octandra*).

No hydathodes were observed.

Eriandra fragrans

WOOD. Growth arcs are present (FIGURE 6). Pores are of uniform size distribution. The arrangement of pore groups is 89.6% solitary, 9.6% clusters, and 0.8% radial multiples. Radial multiples occur in only one of the four specimens studied (*Boschwezen 5810*). Pore outline is circular or slightly angular in some of the narrower vessels. Vessel wall thickness varies from 3.4 to 6.8 μm. Tangential pore diameter averages 180 μm., with a range of 41 to 330 μm. Perforation plates are exclusively simple, generally with round perforations which have only a very slight border

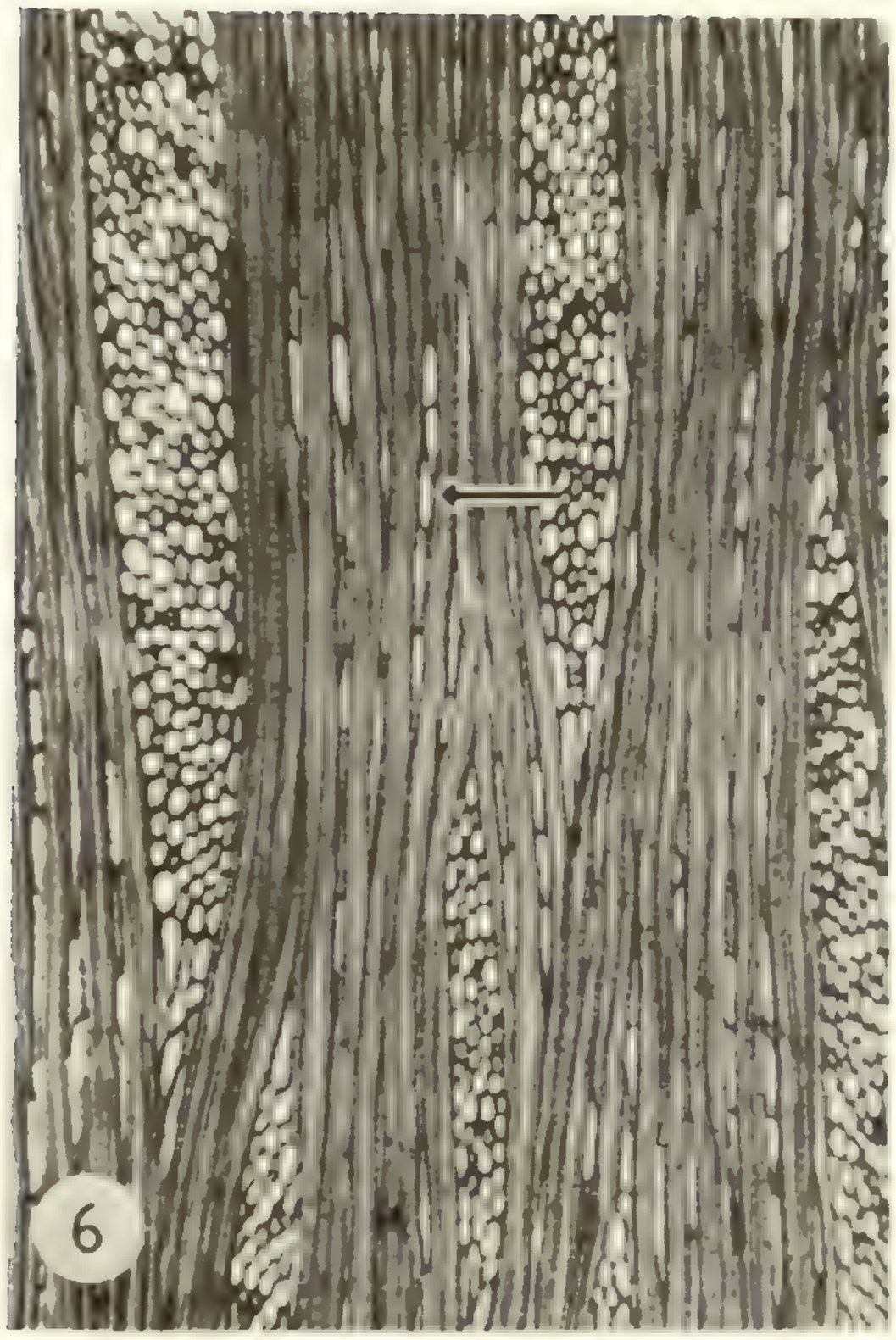
or no border at all. Tyloses are present in some of the specimens (FIGURE 8). In specimens having tyloses, the number varies from few to many per section, and the tyloses are usually abundant in those vessels where present. Both thin-walled and sclerotic tyloses may be present in the same wood. Vessel element length averages 780 μm., with a range of 55 to 1990 μm. Intervascular pitting is alternate; pits are usually oval- or circular-bordered, although there is some range in shape from elongate to nearly polygonal, the latter occurring where pits are crowded. Pit-border diameter ranges from 6.7 to 14 μm. Inner apertures are slitlike and crossed. Vessel element end wall angle ranges from 9° to 89°. Imperforate tracheary elements have a complete range of form from tracheids to distinct fiber-tracheids. The inner aperture does not extend beyond the edge of the border, as is common in fiber-tracheids of woods of many plants. The inner aperture is horizontal in the tracheids, vertical in the fiber-tracheids, and intermediate in position in transitional elements. Imperforate tracheary element wall thickness ranges from 3.4 to 11 μm., with the average length ranging from 340 to 2800 μm. (av. 1453 μm.).

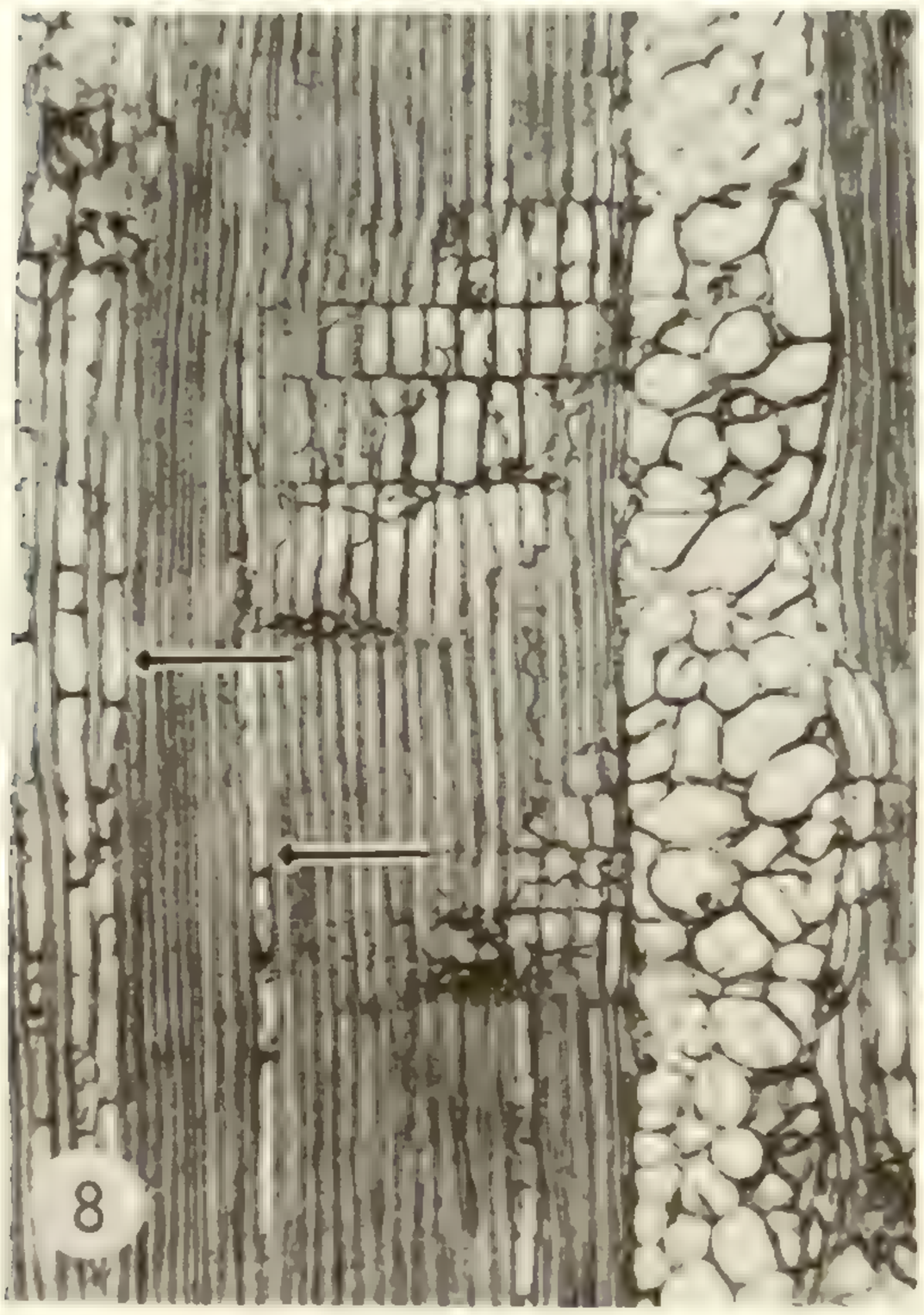
Vascular rays are both homocellular and heterocellular (FIGURES 6, 8). Homocellular rays are largely uniseriate; however, biseriate rays also occur. Homocellular rays vary in width from 14 to 37 μm., and are from 1 to 17 cells (140 to 1920 μm.) high. All cells are erect. Heterocellular rays are mostly multiseriate, but a few biseriate and uniseriate heterocellular rays occur. Ray width varies from 1 to 13 cells (20 to 370 μm.), and height from 6 to 130 cells (380 to 4740 μm.). The body of the heterocellular ray is composed of procumbent cells, with groups of square or short erect cells occurring throughout the ray (FIGURE 4). Uniseriate wings of 1 to 7 tall erect cells are usually present. These long uniseriate wings create some vertically fused rays. The nature of the ray is strongly influenced by the proximity of included phloem (FIGURE 5). The portion of a multiseriate ray produced immediately exterior to a patch of included phloem is much wider than that portion of the same ray at a greater distance from the phloem. For example, a xylem ray that is 10 cells wide next to the included phloem, narrows gradually with increasing radial distance from phloem until its width may be stabilized at only three cells.

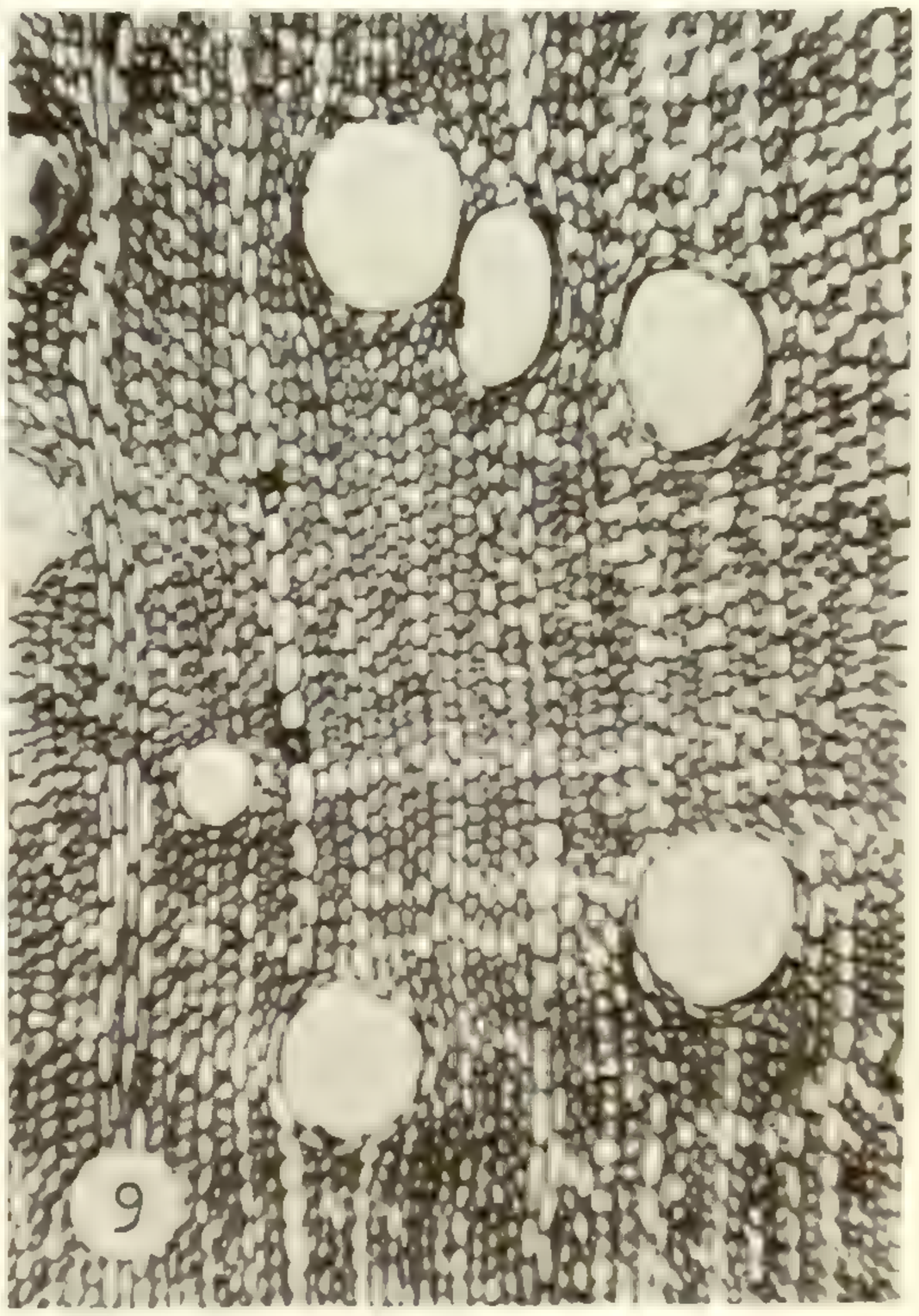
In three specimens, resumption of xylem production following a period of included phloem production was preceded by production of parenchyma which resembles the pith in organization. This loosely organized parenchyma ceases fairly abruptly with resumption of normal xylem production except where a ray arises in the xylem. When this happens, the loosely organized parenchyma extends somewhat into the xylem and, with increasing distance outward from the included phloem, it gradually becomes organized into a ray. The fourth specimen examined had little or no parenchyma of this kind produced between the included phloem and the normal xylem.

Vessel to ray parenchyma pitting is half-bordered. The ray side of the pit-pair usually has a simple pit corresponding to the border on the vessel side. Occasionally, the simple pit on the ray side of the pit-pair is

FIGURE 5: *Eriandra fragrans*, tangential section of stem showing included phloem (between arrows), × 12.







FIGURES 6–9: 6, *Eriandra fragrans*, tangential section of wood showing homocellular uniseriate rays (arrow) and heterocellular multiseriate rays with upright cells along margins and in wings, × 36; 7, *Moutabea longifolia*, radial section of stem showing included phloem (on left side) and a tall heterocellular ray, × 36; 8, *Eriandra fragrans*, radial section of wood showing vessel filled with tyloses, homocellular ray of erect cells, and axial xylem parenchyma (arrows) (note hyphae of fungus in ray), × 36; 9, *Eriandra fragrans*, transverse section of wood showing axial xylem parenchyma distribution (diffuse and tangential apotracheal and paratracheal diffuse with wings are visible), × 36.

larger than the pit on the vessel side. Sometimes the simple pit is large enough to encompass two pits on the vessel side, thus forming a unilaterally compound pit-pair. The vessel side of the pit-pair usually has a circular border and a slitlike inner aperture; sometimes, however, the inner aperture is enlarged to an oval shape.

Polygonal to rhomboid crystals occur in the rays of all specimens of *Eriandra*. Occasionally, in tangential section, erect cells were noted along the sides of the rays, but no real sheath was ever seen.

Axial xylem parenchyma is both apotracheal and paratracheal (FIGURE 9). Apotracheal parenchyma is mostly tangential, but some diffuse parenchyma also occurs. Paratracheal parenchyma is either aliform or paratracheal-diffuse with wings. In vessel to axial parenchyma pitting, the pit-pairs are half-bordered with a circular border and a slitlike inner aperture occurring on the vessel side.

INCLUDED PHLOEM. Included phloem is abundant and can be identified by the presence of sieve tube elements having compound sieve plates. Sclereids occur in the included phloem. Distribution of included phloem is shown in FIGURE 1.

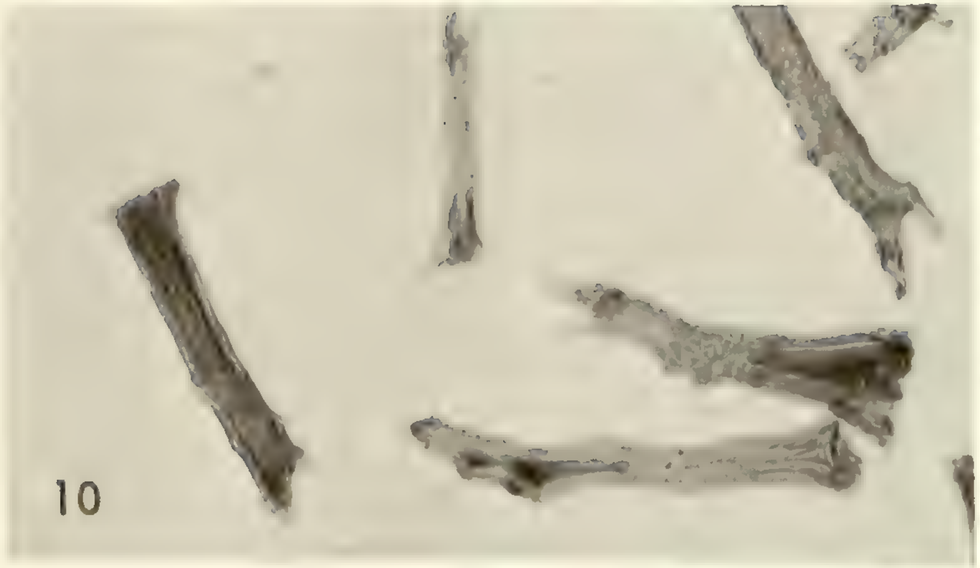
LEAVES. *Eriandra* leaves are simple and unlobed; margins are entire. Venation is brochidodromous. Areolation is mostly well developed and partially oriented. Veinlets are simple or branched, taper gradually to their ends, and are recurved. They consist of fibers with circular-bordered pits. Dense protoplasts are often concentrated at the distal ends of the fibers, but may be absent. Bundle sheath cells, thickened on their inner tangential and radial walls, entirely surround the veinlets.

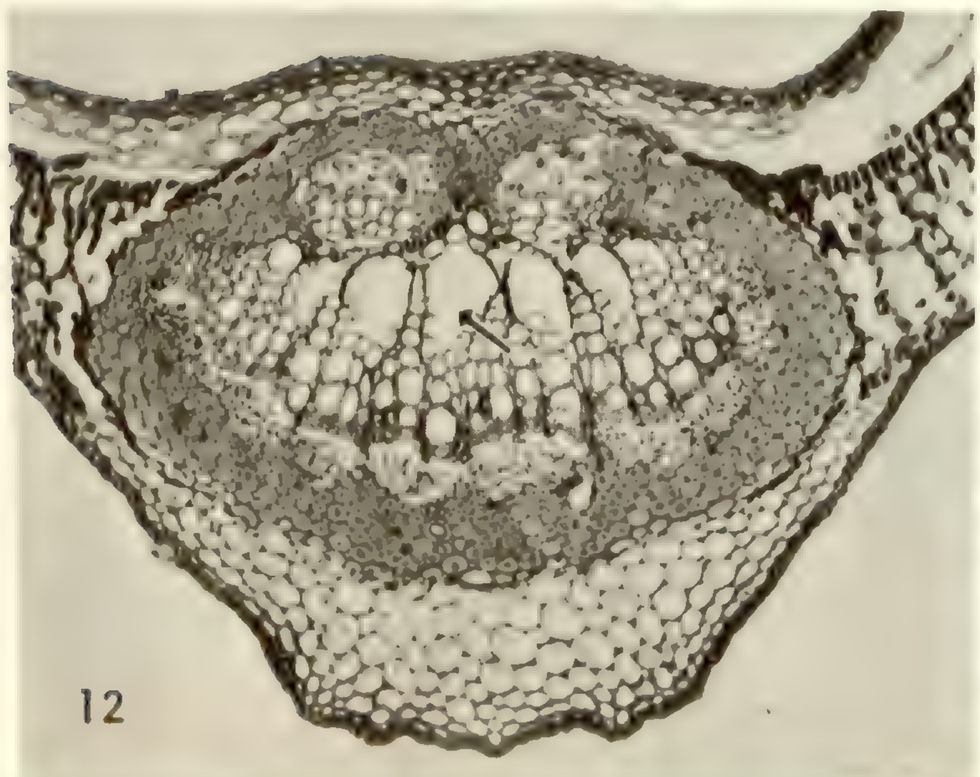
Surfaces of *Eriandra* leaves are flat and the leaves are dorsiventral. The palisade layer is uniseriate with some biseriate areas and is of typical configuration. The spongy layer is of the typical dicotyledonous type, except that some cells in the lower part of the layer have prominent secondary thickenings.

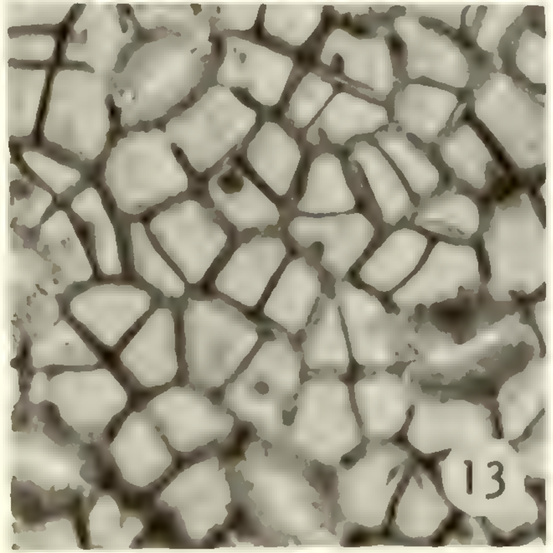
Rhomboid to polyhedral crystals are plentiful in bundle sheath cells and occur regularly in cells of the palisade layer. Similar crystals occasionally occur in cells of the pithlike central area of the primary vein.

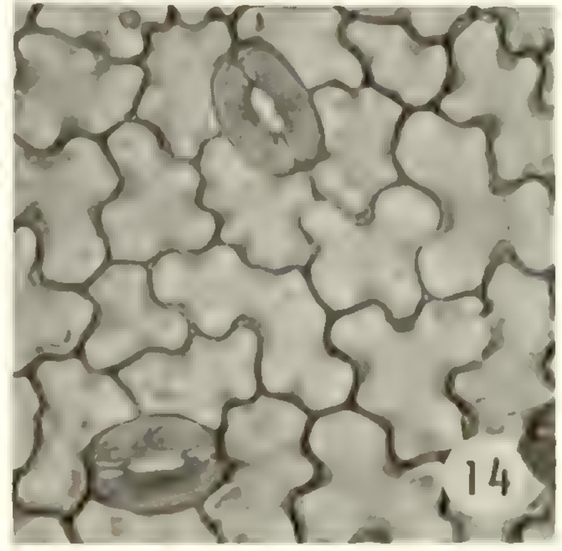
All veins except the primary vein have a single collateral bundle. The primary vein (as seen in transverse section) has a large area of xylem with one long band (or several shorter bands) of phloem adjacent to it on the abaxial side. Adaxial to this large area of xylem and phloem, and separated from it by an area of parenchyma, are one to several smaller xylem areas with phloem flanking each of them on their adaxial sides. Vascular tissue of the primary vein is surrounded by a thin sheath of sclerenchyma. Sometimes a large lacuna is visible in the center of the primary vein. Terminal veinlets lack xylem and phloem.

All veins are ensheathed in fibers that have circular-bordered pits. Although these fibers cannot be classed as either xylem or phloem, they appear to have differentiated from procambium. As the size of the vein









FIGURES 10–14: 10. *Moutabea* sp. (*Wurdack & Adderly 43409*), isolated sclereids from leaf, × 90; 11. *Diclidanthera elliptica*, leaf clearing showing brochidodromous venation, × 6; 12. *Barnhartia floribunda*, transverse section of leaf primary vein showing lacunae (arrow), × 85; 13. *Diclidanthera bolivarensis*, paradermal section of leaf through abaxial epidermis, × 515; 14, *Eriandra fragrans*, paradermal section of leaf through abaxial epidermis, × 375.

decreases, the amount of xylem and phloem decreases until first the phloem is no longer present and then, in the ultimate veinlets, the xylem is also absent, leaving only the fiber sheath surrounded by the bundle sheath. Bundle sheath cells are thickened on their radial and inner tangential walls and ensheath all vein sizes. Bundle sheath extensions are absent.

The lower epidermis is uniseriate; the upper epidermis is either uniseriate or biseriate.

In face view, epidermal cells of both leaf surfaces are sinuous (FIGURE 14). The amount of waviness varies according to the specimen, from slightly to moderately wavy. The outer layer of the adaxial epidermis differs from the inner layer in two ways: the inner layer has larger cells, and the anticlinal walls of its cells are straight or are less sinuous than those of the outer layer.

In sectional view, epidermal cells are square to rectangular. The cuticle is smooth-surfaced, varying in thickness from 1.4 to 2.7 μm.

Stomata are restricted to the lower epidermis and are evenly distributed over its surface. The stomatal apparatus is anomocytic (FIGURE 14). Guard cells are reniform; a pair elliptical (length/width = 1.32). They are provided with a prominent outer cuticular ridge which projects from the guard cell over the stoma, parallel with the surface of the leaf. An inconspicuous inner ridge is also present. A cross section through the guard cells reveals thin anticlinal walls and thickened periclinal walls.

No trichomes or hydathodes were observed.

Moutabea

WOOD. Faint growth arcs occur; pores are of uniform size distribution. Pore distribution is mostly solitary (80–92%, average for all species 85%) with a substantial fraction of pore clusters (8–18%, average for all species 14%) and a few radial pore multiples (0–3%, average for all species 1.4%). One very young portion of the wood of *Moutabea* sp. (*Wurdack & Adderly 43409*) has 91% solitary and 9% radial pore multiples. Pore outline is circular to somewhat angular in the smaller vessels. Vessel wall thickness varies from 3.4 to 9.5 μm. Tangential pore diameter averages 180 μm. with a range of 34 to 360 μm. Perforation plates are simple; borders are absent or vestigial on the round perforations. Tyloses are present and vary from thin-walled to thick-walled. The lumina of the tyloses may be nearly occluded in those having the thickest walls. The number of tyloses varies from few to many per section and from few to many per vessel. Vessel element length averages 620 μm., with a range of 110 to 1440 μm. Variation in length within a species is as great as that between species. For example, average vessel element lengths for three specimens of *M. guianensis* are 550 μm., 580 μm., and 750 μm.; for the single specimens of *M. longifolia* and *Moutabea* sp. (*Wurdack & Adderly 43409*), 610 μm. and 540 μm., respectively. Intervascular pitting is alternate; pit borders are circular to oval, sometimes grading to polygonal. The diameter

of the pit border ranges from 7.4 to 12 μm. Inner apertures are slitlike and only slightly crossed. Vessel element end wall angle ranges from 1° to 89°. Imperforate tracheary elements vary from tracheids to fiber-tracheids. Pits of the imperforate tracheary elements are circular-bordered with slitlike apertures; wall thickness varies from 2.7 to 9.5 μm.; cell length varies from 340 to 1440 μm. (av. 890 μm.).

Vascular rays are both homocellular and heterocellular. Homocellular rays are nearly all uniseriate, ranging from 7 μm. wide in the uniseriate rays to 29 μm. in some of the biseriate rays. Biseriate rays usually have extensive uniseriate wings. Height of homocellular rays varies from 1 to 15 cells (51 to 1130 μm.). Heterocellular rays are mostly biseriate or multiseriate, but may vary in width from 1 to 16 cells (10 to 410 μm.). Height varies from 3 to 138 cells (140 to 5640 μm.). Vertically fused rays are common, as are uniseriate wings. Cells of heterocellular rays range from procumbent to square to upright (FIGURE 7); uniseriate wings are formed of upright cells.

Proximity of xylem rays to included phloem influences their structure as follows: immediately external to included phloem, the xylem consists of areas of homogeneous, pithlike parenchyma; with increasing radial distance from the included phloem, this xylem parenchyma gradually becomes organized into indistinct rays by the intercalation of imperforate tracheary elements among the parenchyma cells; finally, it is organized into the distinct rays characteristic of typical xylem.

Vessel to ray parenchyma pitting is half-bordered; the vessel side of the pit-pair has a circular border and a slitlike inner aperture, the ray side a simple pit corresponding to the border on the vessel side. Inner apertures of closely adjacent pit-pairs are often fused into one large aperture. Rhomboid to polyhedral crystals occur in rays of *M. guianensis* and *Moutabea* sp. (*Wurdack & Adderly 43409*) but are not present in *M. longifolia*. The fluid-preserved specimen of *M. guianensis* contains several types of deposits in ray cells: some cells have a large sphere, others many small spheres, and others granular masses. The chemical composition of these deposits is not known. Spherical starch grains were identified using polarized light. Some upright cells occur on the periphery of the ray, but no definite sheath of cells is present.

Both apotracheal and paratracheal axial xylem parenchyma are present. Apotracheal parenchyma is diffuse or tangential. Paratracheal parenchyma is mostly diffuse with wings, although a little aliform parenchyma is present. In *M. guianensis* aliform parenchyma is the major type of axial xylem parenchyma encountered in immature wood produced prior to the first included phloem. Crystals do not occur in the axial parenchyma; starch grains were seen in fluid-preserved wood. Vessel to axial parenchyma pitting is half-bordered, with the border occurring on the vessel side of the pit-pair.

INCLUDED PHLOEM. Included phloem is distributed in crescent-shaped, more or less concentric segments and may be identified by the presence of

sieve tube elements with compound sieve plates. Fibers and sclereids also occur.

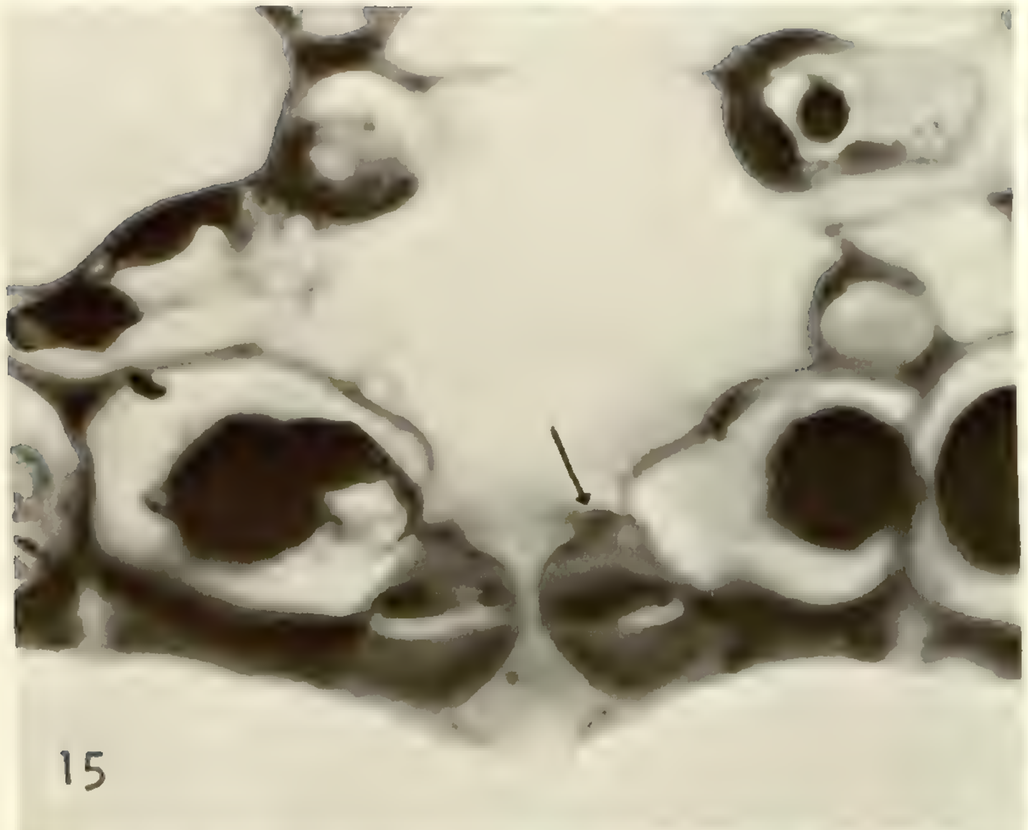
LEAVES. *Moutabea* leaves are simple and unlobed; margins are entire. Venation is brochidodromous. Areolation is mostly well developed and partially oriented. Veinlets are simple or branched, have clavate endings, and are not recurved. They consist of large, thin-walled, expanded, spirally thickened tracheary elements (probably tracheids). The last element in the veinlet is often expanded greatly, sometimes being almost spherical; it is usually associated with a columnar sclereid (FIGURE 16). Unthickened bundle sheath cells entirely encase the veinlets.

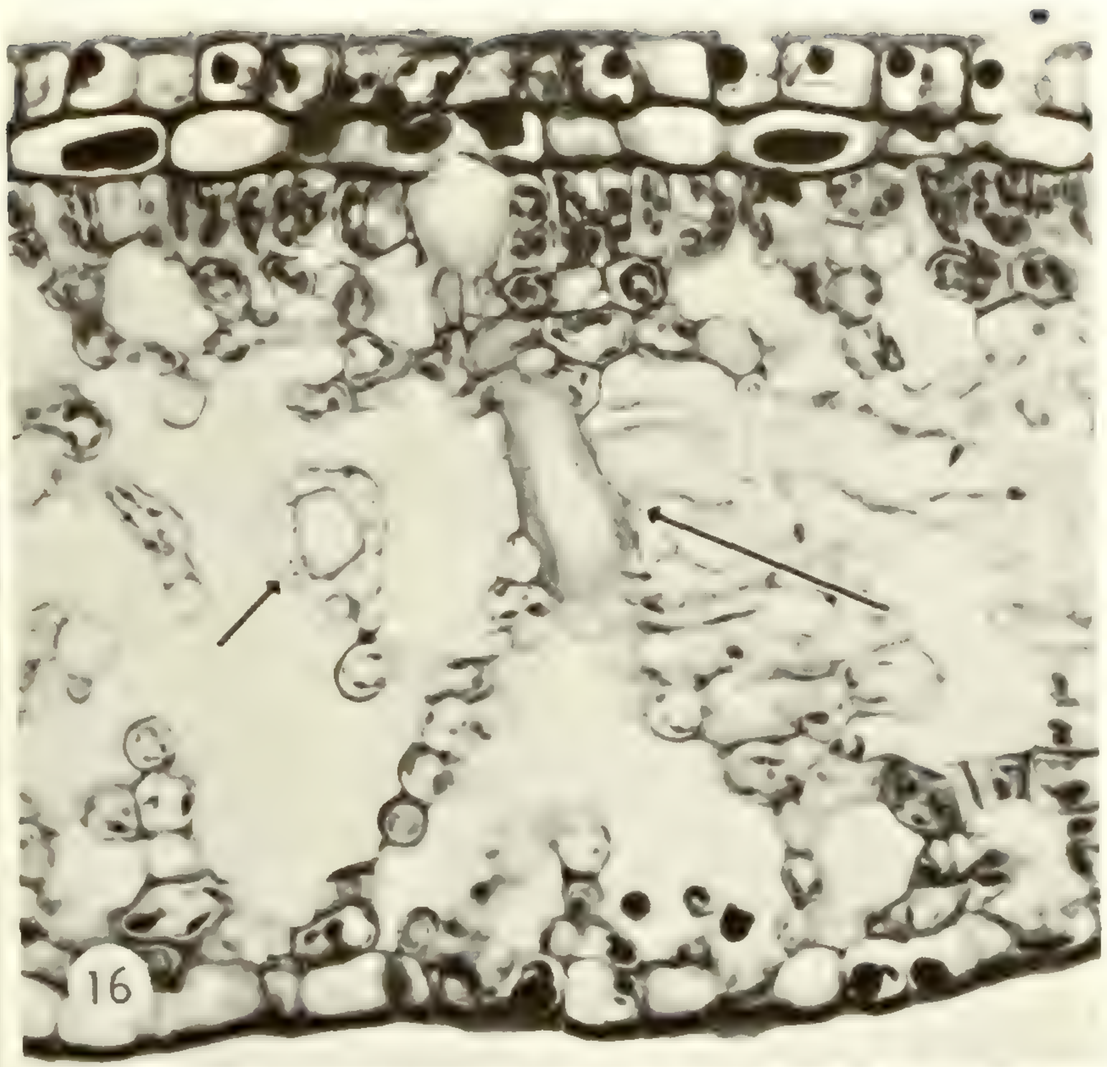
Surfaces of *Moutabea* leaves are flat. Leaves are dorsiventral. The palisade layer is usually uniseriate or biseriate. However, *Moutabea* sp. (*Wurdack & Adderly 43409*) has a third layer transitional between palisade and spongy layers; *M. excoriata* is triseriate; one specimen of *M. guianensis* (*Van Donselaar 3193*) is multiseriate, having from four to five tiers of cells in the palisade layer. The spongy layer is the usual lacunose type.

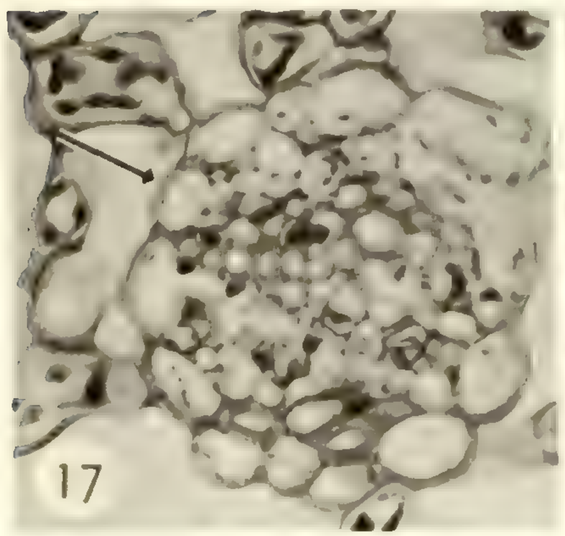
Rhomboid and polyhedral crystals occur in *M. aculeata*, *M. excoriata*, and *M. guianensis*, but not in *M. longifolia*. These crystals occur in bundle sheath cells of *M. aculeata* and *M. guianensis*. Some of the species have similar crystals in cells of the palisade and spongy layers. Druses occur in idioblasts in the palisade layer of *Moutabea* sp. (*Wurdack & Adderly 43409*). Spherical aggregations of small anisotropic particles embedded in dark, isotropic, amorphous masses occur in cells of the spongy layer of *M. longifolia* and in cells of the lower epidermis of *M. guianensis*. The insolubility of this material in dilute HCl indicates that it is neither calcium oxalate nor calcium carbonate, two crystalline substances commonly found in plant cells.

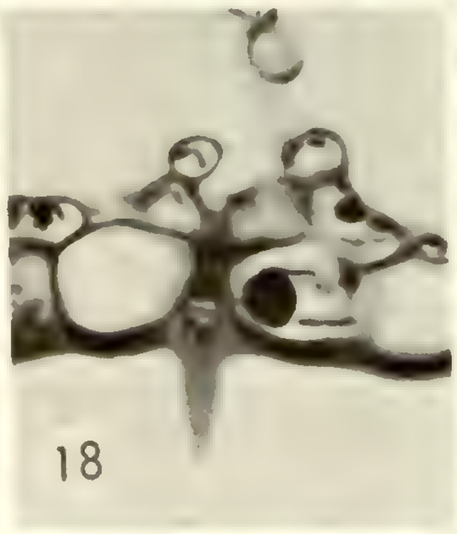
Vascular bundles vary in construction with size. The primary vein differs slightly among species. Basically, as seen in transverse section, it consists of a large area of xylem flanked by phloem in the normal abaxial position. In addition, there are one or sometimes two or three smaller areas of xylem flanked by adaxial phloem over the main vascular supply noted above. Parenchyma extending laterally from one side of the vascular bundle to the other creates a central pithlike region. All of this is surrounded by one to three layers of sclerenchyma cells. In *Pulle 389* (*M. guianensis*), xylem areas are joined, and are surrounded by phloem, to form a ring of xylem surrounded by a ring of phloem with parenchyma in the middle. Medium-sized veins consist of a collateral bundle surrounded by a bundle sheath whose cells are thickened on the outer tangential and radial walls (FIGURE 17). The smallest veins lack phloem, and the bundle sheath cells are not usually thickened. Bundle sheath extensions are absent.

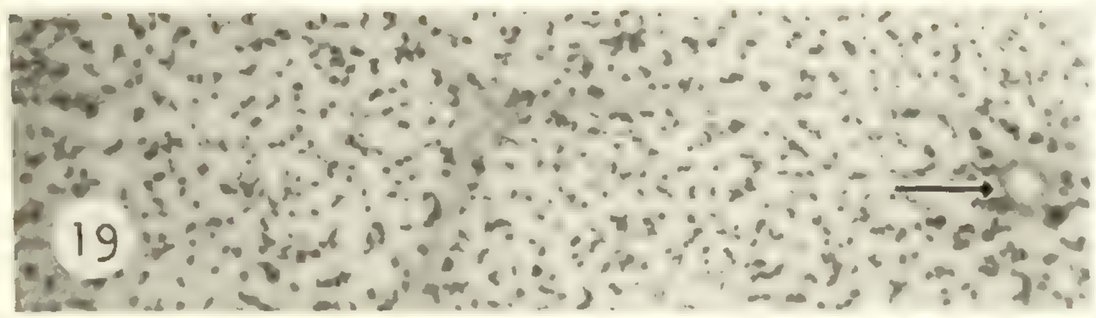
The lower epidermis is uniseriate. The upper epidermis is three to four layers thick over the primary vein, tapering quickly to one or two layers over the rest of the blade. Two specimens of *Moutabea guianensis* have











FIGURES 15–19: 15, *Moutabea guianensis*, leaf transverse section through abaxial epidermis showing median cross section of stomatal apparatus (note inner ledge on guard cell (arrow)), × 1050; 16, *Moutabea guianensis*, transverse section of leaf showing terminal position of sclereid (long arrow) and bundle sheath around terminal veinlet (short arrow), × 240; 17, *Moutabea guianensis*, transverse section of leaf showing cross section of medium-sized vein (note unevenly thickened bundle sheath cells (arrow)), × 360; 18, *Moutabea guianensis*, transverse section of leaf showing hair on abaxial epidermis, × 360; 19, *Moutabea guianensis*, leaf clearing showing distribution of sclereids (black dots) (note nectary on abaxial surface (arrow)), × 13.

a uniseriate upper epidermis; a third specimen has a biseriate epidermis. Thus, the number of epidermal layers cannot have much importance in distinguishing species.

In face view, the epidermal cells of both leaf surfaces are polygonal. In *M. guianensis* and *M. longifolia*, cells of the second epidermal layer are noticeably larger than those of the outer layer. The epidermal cells of *M. excoriata* and *Moutabea* sp. (*Wurdack & Adderly 43409*) are approximately the same size in both layers. The *Wurdack & Adderly* specimen is unique among the moutabeas studied, in possessing paired epidermal cells similar to those described in *Barnhartia*. These paired cells differ from those in *Barnhartia*, however, because they occur in the inner instead of the outer epidermal layer.

In sectional view, epidermal cells are square to rectangular. Often cells of the outer layer of the upper epidermis are elongated perpendicularly to the plane of the leaf. Cuticle thickness usually varies from 1.4 to 4.1 μm. and is occasionally as thick as 5.4 μm.

Stomata are restricted to the lower epidermis and are evenly distributed. The stomatal apparatus is anomocytic. Guard cells are reniform; a pair is roughly circular (length/width = 0.97). The guard cells possess a prominent outer cuticular ridge which usually extends parallel with the plane of the leaf or sometimes projects slightly above the leaf surface. A less prominent inner ridge is also present (FIGURE 15). In median transverse section, guard cells have heavily thickened periclinal walls and thin anticlinal walls.

Trichomes are present in small numbers on the lower epidermis of *M. guianensis* (FIGURE 18) and in very small numbers (2 trichomes in 54 transverse sections) on the lower epidermis of *M. excoriata*. Trichomes are similar in both species and consist of outgrowths of epidermal cells. They extend above the leaf surface to a height about equal to the thickness of a normal epidermal cell. No trichomes were observed in the other species of *Moutabea*.

No hydathodes were observed.

All species of *Moutabea* possess columnar sclereids in the leaves. Sclereids are variously thickened; often the lumen is nearly occluded. Walls consist of many concentric lamellations easily visible both with and without polarized light. Generally, the adaxial end of a sclereid is truncated, while the abaxial end tapers to a point (FIGURE 10). Sclereids of different species show various degrees of branching and various densities within the leaf (FIGURE 19). The adaxial ends of the sclereids usually terminate just inside the inner layer of the upper epidermis. Where more than one epidermal layer is present, some small branches of the sclereid usually penetrate to the inner side of the external layer of epidermal cells. The abaxial ends of the sclereids usually terminate in the spongy layer close to the lower epidermis. Sclereids are regularly associated with terminal veinlets and may therefore be called "terminal sclereids" (FIGURE 16).

DISCUSSION AND CONCLUSIONS

Wood Anatomy of Moutabeae

Woods of the Moutabeae are very homogeneous and no clear differences in xylem that might be used to separate the genera can be distinguished. This fact is clear even though two of the genera studied are represented by very immature material. Several xylem characteristics are common to the tribe. Growth arcs are present in all material except the immature specimens of *Diclidanthera penduliflora* and *Barnhartia*. Pores are uniformly distributed and overwhelmingly solitary (80–90%), but clusters also occur in all genera except in the immature specimens of *Barnhartia*. In the wood of *Moutabea* sp. (*Wurdack & Adderly 43409*), for example, pore clusters do not appear until after the first segments of included phloem are produced. Pores are generally round to slightly angular in some of the narrower vessels. Pore diameter shows no significant differences among genera that can not be attributed to age variations in the wood samples (Cumbie, 1960). For example, in *Moutabea* sp. (*Wurdack & Adderly 43409*), average pore diameter is 62 μm. inside the first-formed included phloem and 120 μm. in later-formed wood. Average pore diameters in young wood of *Barnhartia* and *Diclidanthera* (48 μm. and 46 μm., respectively) are similar to average pore diameters interior to the first-formed included phloem in *Moutabea* sp. (*Wurdack & Adderly 43409*). While average pore diameters for *Moutabea* (180 μm. and *Eriandra* (180 μm.) as a whole are higher than for *Moutabea* sp. (*Wurdack & Adderly 43409*), I do not believe this is significant, especially in light of total variation in pore size of mature wood (e.g., 34 to 360 μm. in *Moutabea*).

Perforation plates are exclusively simple with round perforations. That tyloses occur in *Eriandra* and *Moutabea* and are absent in *Diclidanthera* and *Barnhartia* is most likely another reflection of variation with age. Differences in vessel element length can be attributed to sample habit (tree, vine, shrub), sample source (location in the plant), and sampling error (Bailey & Tupper, 1918; Carlquist, 1961). The same may be said of pit diameter, vessel element end wall angle, and imperforate tracheary element length.

Intervascular pitting is alternate; pits are usually circular-bordered but may become polygonal when closely spaced. Imperforate tracheary elements range from tracheids to fiber-tracheids. Vascular rays may be homocellular or heterocellular. Homocellular rays are mostly uniseriate, occasionally biseriate, and vary in height from 1 to 15 cells. Heterocellular rays are uniseriate to multiseriate, occasionally up to 16 cells in width, may surpass 100 cells in height, and commonly have long uniseriate wings. Again, structural differences among genera may be attributed to variables of sample source, age, and species habit (Carlquist, 1961). Diffuse and tangential apotracheal, and diffuse paratracheal with wings are the main types of axial xylem parenchyma. Arcs or partial rings of

included phloem are present in all genera except *Barnhartia*. I strongly suspect older wood of *Barnhartia* would also display included phloem since overall growth and appearance of *Barnhartia* closely resembles that of other woody climbers in the family (Sprague & Sandwith, 1932).

The term "conjunctive tissue" has been used to refer to parenchyma associated with included phloem (Chalk & Chattaway, 1937; Eames & MacDaniels, 1947; Committee on Nomenclature, 1957; Fahn, 1974), and does not indicate whether such tissue had its origin in xylem or phloem. Since "conjunctive" parenchyma in Moutabeae is clearly xylem parenchyma, use of the term "xylem parenchyma" is preferable: it is more informative than the noncommittal term "conjunctive" parenchyma and it is not liable to misinterpretation.

The types of axial parenchyma present in Moutabeae are difficult to identify and place into established categories. This is because of the irregular configuration of the wood caused by the included phloem. Consequently, anatomists have not been consistent in their descriptions of axial xylem parenchyma in Moutabeae. Metcalfe and Chalk (1950) state that *Moutabea* has predominantly diffuse or banded apotracheal parenchyma, Biswas (1969) reports diffuse-in-aggregates apotracheal and scanty paratracheal, and Record and Hess (1943) report metatracheal (banded apotracheal) and vasicentric paratracheal. Comparison of these descriptions with mine (diffuse and tangential apotracheal, paratracheal diffuse with wings, and a small amount of aliform paratracheal parenchyma) shows that most of the inconsistencies arise either from different terminologies used by other botanists or from their failure to include one or more types of parenchyma in their description. The outstanding differences between my descriptions and those of other botanists is my report of wings associated with the diffuse paratracheal parenchyma and of the presence of aliform parenchyma.

Hegnauer (1969) has noted in several families (e.g., Iridaceae, Gramineae, Labiatae) that tropical members store starch while temperate members store carbohydrates other than starch. Since he found copious amounts of starch in *Securidaca*, a tropical member of the Polygalaceae, and none in a number of temperate members, he suggests that a parallel situation may exist in the Polygalaceae. According to Hegnauer's hypothesis, all members of the Moutabeae should store starch. However, starch was observed in only one specimen, the sole fluid-preserved specimen.

Leaf Anatomy of the Moutabeae

Although the leaves of the Moutabeae show greater structural variation than the xylem, there is, nevertheless, a basic leaf structure characteristic of the tribe. Leaves are simple and unlobed with entire margins. Venation is brochidodromous; areolation is mostly well developed and partially oriented. Veinlets are simple or branched and encased in bundle sheaths. Bundle sheath extensions are absent. No hydathodes are present.

Surfaces of the leaves are flat with no pronounced topographic features.

Leaves are dorsiventral. A palisade layer 1 to 3 cells high and a well-developed lacunose spongy layer are present. Rhomboid to polyhedral crystals occur in bundle sheath cells of some species in all genera. All veins except primary veins have single collateral bundles. Veinlets lack phloem. Primary veins are large and appear to be constructed of a large collateral bundle which is separated from one or more smaller, inverted adaxial bundles by varying amounts of parenchyma.

The lower epidermis is uniseriate. The upper epidermis has biseriate regions in all species; in some species it may be triseriate.

Stomata are restricted to the lower epidermis. The stomatal apparatus is anomocytic. Guard cells are reniform and possess a prominent outer cuticular ridge; they have thickened periclinal walls and thin anticlinal walls.

There is a distinct difference between *Eriandra* leaves and those of the other three genera. In *Eriandra* leaves, vein endings taper, are recurved, and consist of fibers with bordered pits in the walls; epidermal cells are sinuous in outline and do not occur in pairs; guard cell pairs are elliptical (length/width ratio 1.3); and some parenchyma cells of the spongy mesophyll have prominent secondary thickenings. On the other hand, in *Barnhartia*, *Diclidanthera*, and *Moutabea* leaves, vein endings are clavate, straight, and composed of enlarged, spirally thickened tracheary elements; epidermal cells are polygonal in outline; paired epidermal cells occur in all species of *Barnhartia* and *Diclidanthera*, and in *Moutabea* sp. (*Wurdack & Adderly* 43409); guard cell pairs are round (length/width ratio 0.97–1.01); and parenchyma cells of the spongy mesophyll lack prominent secondary thickenings. Van Royen and van Steenis (1952) report a distribution for extrafloral nectaries which supports the separation of *Eriandra* from the other three genera: absent in *Eriandra*; present in *Barnhartia*, *Diclidanthera*, and *Moutabea*. Although I have not made a thorough study, I have observed extrafloral nectaries in *Barnhartia* at the distal end of the petiole, in *Diclidanthera* at the base of the blade, and in *Moutabea* on either side of the stem where the petiole is attached, as well as on the abaxial leaf surface.

While *Barnhartia*, *Diclidanthera*, and *Moutabea* form a group distinct from *Eriandra*, the group is not entirely homogeneous. For example, leaves of all species of *Moutabea* contain numerous columnar sclereids; similar sclereids are absent in *Barnhartia* and *Diclidanthera* (as well as in *Eriandra*). *Moutabea* differs from *Barnhartia* and *Diclidanthera* in two additional ways: first, while all species of *Barnhartia* and *Diclidanthera* have paired cells in the outer epidermal layer of the leaf, only one species of *Moutabea* (*Moutabea* sp. (*Wurdack & Adderly 43409*)) has paired epidermal cells, and these only occur in the inner epidermal layer; second, in *Moutabea*, bundle sheath cells are thickened on their outer periclinal walls, while in the other genera of Moutabeae, bundle sheath cells are thickened on the inner periclinal walls. *Barnhartia* and *Diclidanthera* leaves are too similar to separate anatomically.

Anatomy is seldom useful in separating species (Metcalfe & Chalk,

1950; Bailey, 1953), as is generally true here. However, the columnar sclereids of *Moutabea* offer a possible means of species discrimination (Foster, 1946, 1947; Rao, 1951, 1957). Foster's (1946) study of *Mouriria* Aublet (Melastomataceae) shows the extent to which sclereids can vary in a genus, and how this variation can be used to group species. However, Foster's study of foliar sclereids in *Trochodendron aralioides* Sieb. & Zucc., which reveals the ". . . remarkable fluctuation in the form and structure of such cells which can occur within a single species" (Foster, 1946), indicates that sclereids may not necessarily be useful taxonomically. While sclereids in different specimens of *Moutabea* differ slightly in branching and concentration, no consistent patterns could be detected.

Evolutionary Trends and Phylogenetic Relationships

According to Carlquist (1961) and others, vessel element specialization is the most reliable guide to evolutionary trends in the xylem. Primitive woods are those whose vessel elements most resemble tracheids (i.e., long, narrow, scalariformly pitted cells with scalariform perforation plates and angular transverse sections). Advanced woods are those whose vessel elements are short, broad, alternately pitted cells with simple perforation plates and round transverse sections. Many other features of xylem have been ranked as primitive or advanced by correlation with the degree of vessel element specialization (e.g., solitary pores, long imperforate tracheary elements, and lack of libriform wood fibers are considered primitive). Based on the following characteristics of *Eriandra* and *Moutabea* wood (these being the only genera for which mature wood was available), the Moutabeae appear to be intermediate, neither primitive nor very advanced. Vessel element length averages ca. 700 μm., which is very near the 649 μm. average found for 600 dicotyledons (Metcalfe & Chalk, 1950). Pore diameters average 180 μm., as compared to 94 μm. for 1500 dicotyledons (Metcalfe & Chalk, 1950). Pores are mainly solitary (87%; 12% occur in small clusters) and are round in outline. Intervascular pitting is alternate; perforations are simple. Imperforate tracheary elements, which consist of tracheids and fiber-tracheids, average 1170 μm. in length, as compared to 1317 μm. for 534 dicotyledons (Metcalfe & Chalk, 1950).

Acceptance of the evolutionary state of advancement indicated by these facts should be tempered by the realization that phylogenetic relationships may be masked by specializations related to a specific habit. This is effectively demonstrated by comparison of my study of Moutabeae with the Ayensu and Stern (1964) study of Passifloraceae. By comparing arboreal and lianous members of this family, they demonstrated that the following characters are correlated with the lianous habit: anomalous growth; short vessel elements; broad, solitary vessels; perforated fiber-tracheids; and absence of libriform wood fibers. This is remarkably similar to the situation in Polygalaceae tribe Moutabeae, which has short, broad vessel elements, and solitary vessels. While there are no perforated fiber-tracheids in the Moutabeae, there are long, narrow vessel elements

with very oblique end walls which might be described as "perforated tracheids" and which appear similar to the perforated fiber-tracheids of the Passifloraceae.

Significantly, *Eriandra*, whose wood shows all the lianous characters above, is a tree up to 25 meters tall and nearly a meter in diameter. The possession of anatomical traits normally associated with lianas might suggest they are structural relicts indicative of a lianous ancestry and might provide independent evidence that *Eriandra* is related to the other lianous members of the Moutabeae. Arboreal habit and somewhat longer, more specialized imperforate tracheary elements could indicate that *Eriandra* is diverging from the rest of the Moutabeae. Evidence from the leaves, which has been previously noted, strengthens the contention that *Eriandra* is becoming separated from the other genera of the tribe. That *Eriandra* should have diverged is not surprising considering its geographical separation from the other genera. This divergence can only be tentatively suggested since the changes noted are slight and might be associated with other variables such as habit or sampling.

No major evolutionary trends similar to those developed for secondary xylem have been developed for leaves. Perhaps this is because leaves vary so readily in response to habitat. However, because leaves seem to evolve faster than wood, they are often useful for studying evolutionary trends within families or genera (Carlquist, 1961; Tucker, 1964). On the morphological level, Hickey's (1973) study of leaf architecture promises to provide botanists with another means of studying plant phylogeny and evolution. He has found most dicotyledonous taxa to possess consistent patterns of leaf architecture. Although I have not made a detailed analysis of leaf architecture in Moutabeae, all genera appear alike superficially in that they have simple, entire leaves with brochidodromous venation.

Several anatomical features of leaves have been used as indicators of genetic relationships. As mentioned earlier, Moutabeae have similar mesophyll structure, crystals, bundle sheaths, vascular bundles (including primary veins), epidermal structure, and stomatal apparatus, all of which indicate that these genera might have had a common origin. There are also smaller differences, probably the result of evolution within the tribe, which allow the separation of *Eriandra* from *Barnhartia*, *Diclidanthera*, and *Moutabea*, and the separation of *Moutabea* from *Barnhartia* and *Diclidanthera*. *Eriandra* displays the greatest number of differences; *Moutabea* differs from the other genera in its columnar foliar sclereids.

Separation of *Eriandra* from the rest of the tribe is strengthened by study of the evolutionary origin of terminal columnar sclereids. Cells which occur at the terminus of a veinlet are referred to as "terminal" cells, e.g., terminal sclereids (Foster, 1946, 1947, 1956; Tucker, 1964). Foster (1946) first noted the restriction of sclereids to the ends of veinlets in his study of *Mouriria*. Terminal cells may either be normal conductive cells or idioblasts, the latter being referred to as "terminal idioblasts" (Tucker, 1964). If these idioblasts resemble tracheids in having spirally thickened or pitted walls, but differ from typical tracheids in form, size,

or general topography, they are termed "tracheoid idioblasts" (Foster, 1956). Tucker (1964) suggests that terminal cells show phylogenetic trends of specialization analogous with the evolutionary development of vessel elements and imperforate tracheary cells. Terminal sclerenchymatous idioblasts and terminal tracheoid idioblasts are believed to represent cell types which have evolved from normal conductive terminal vascular cells. Although ontogenetic studies such as those of Foster (1944, 1945) would be necessary to prove the procambial origin of sclerenchymatous idioblasts in Moutabeae, my own observations and those of Foster (1947) on the terminal nature of these cells argue strongly for their procambial origin. I have refrained from using the term "tracheoid idioblast" and have instead referred to such cells as "enlarged. spirally thickened tracheary elements." I have done this because I believe that the morphology and distribution of these cells does not warrant calling them idioblasts, and because they definitely look like tracheary elements and are not merely tracheoid. The presence of enlarged terminal tracheary cells in *Barnhartia*, *Diclidanthera*, and *Moutabea* indicates a tendency for change in the terminal cells of veins in these genera, providing additional evidence for the presumed relationship among *Barnhartia*, *Diclidanthera*, and *Moutabea*, and confirming their separation from *Eriandra*.

In summary, the phylogeny of the tribe, based on anatomical evidence, indicates that *Barnhartia*, *Diclidanthera*, and *Moutabea* are more closely related to one another than they are to *Eriandra*. In addition, *Barnhartia* and *Diclidanthera* are more closely related to each other than to *Moutabea*. These conclusions agree with the assessment (based on floral morphology) of van Royen and van Steenis (1952), except for their consideration of *Diclidanthera* as closely related to *Eriandra*.

The anatomical evidence supports several taxonomic conclusions. First, it seems quite clear that the genera of Moutabeae are all polygalaceous. For example, in both Moutabeae and other Polygalaceae, some genera have stems with similar types of anomalous growth. Both groups also possess solitary vessels with simple perforation plates, alternate intervascular pitting, and imperforate tracheary elements with bordered pits (Metcalfe & Chalk, 1950; Biswas, 1969). Leaves of both groups are similar in possessing unicellular or multicellular uniseriate hairs, epidermides with generally straight anticlinal walls, and generally anomocytic stomatal apparatuses (Metcalfe & Chalk, 1950). Crateriform extrafloral nectaries or glands are also distributed throughout the family. In my opinion, these anatomical features provide a basis for strong arguments against further usage of Diclidantheraceae to represent a group separate from Polygalaceae. This is especially true if, as in Metcalfe and Chalk (1950), *Barnhartia* is treated under Polygalaceae, since *Barnhartia* and *Diclidanthera* are practically indistinguishable anatomically.

A second taxonomic conclusion sustained by anatomical evidence is that the genera of Moutabeae are homogeneous enough to warrant being placed in a single tribe. However, it is not yet certain that anatomy would sub-

stantiate the tribal lines now drawn by taxonomists in the Polygalaceae. For example, Hutchinson (1967) and others place *Bredemeyera* Willd. and *Securidaca* L. in the tribe Polygaleae. Both of these are lianous genera with anomalous secondary growth very similar to that in Moutabeae (Müller, 1866; Crüger, 1850; Chodat, 1896; Schenck, 1893; Metcalfe & Chalk, 1950). Further anatomical study of these and other genera of Polygalaceae would be needed to test the tribal boundaries. If further study revealed that the Polygaleae and Moutabeae are too similar to be separated anatomically, the present morphologically based distinction between the tribes would be weakened. On the other hand, if further anatomical study revealed differences among members of the tribes, present tribal distinctions would be strengthened. It would be more likely that basic differences would be discovered in the leaves of the lianous genera than in the stems, since the structure of stems may reflect the peculiar mechanical and physiological demands of lianous habit rather than any genetic relationships.

Finally, my work bears out Perkins's (1907) exclusion of *Diclidanthera* from the Styracaceae, because the Styracaceae almost universally possess scalariform perforation plates and often have stellate hairs (Solereder, 1908), while *Diclidanthera* shows only simple perforation plates and uniseriate hairs.

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EBENACEAE HARDY IN TEMPERATE NORTH AMERICA [1]

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EBENACEAE Gürke in Engler & Prantl, Nat. Pflanzenfam. IV. 1: 153. 1891, nom. cons.

(EBONY FAMILY)

Evergreen or deciduous trees and shrubs, usually with very hard, blackish wood and watery sap. Leaves simple, alternate or rarely opposite or whorled, exstipulate, mostly with entire margins, the venation pinnate. Flowers actinomorphic, imperfect (and the plants dioecious or sometimes monoecious), or sometimes occasional flowers perfect (and the plants polygamous or polygamodioecious); staminate flowers usually in few-flowered, axillary, cymose inflorescences; carpellate flowers axillary, usually solitary. Calyx synsepalous, articulated at base, 3–7-lobed, often accrescent in age. Corolla sympetalous, 3–7-lobed, the lobes usually contorted, imbricate (or rarely valvate) in bud. Stamens usually 2 or 3 times the number of corolla lobes, epipetalous (or rarely hypogynous), in 2 or more whorls, the filaments free or connate, the anthers 2-loculate; in carpellate flowers the androecia reduced to staminodia or absent. Gynoecium syncarpous, the styles connate for all or a portion of their length; ovary superior, 2–16 (–20)-locular, each locule with 1 or 2 pendulous, anatropous, bitegmic ovules; in staminate flowers the gynoecia vestigial or absent. Fruit a berry, often succulent, usually subtended by the persistent calyx. Seeds with thin coats, the straight or slightly curved embryos with foliaceous cotyledons, embedded in copious cartilaginous or sometimes ruminate endosperm. (Guaiacanae Jussieu, Diospyraceae Novak; including Lissocarpaceae Gilg; excluding Onocatheaceae Kobuski ex Airy Shaw.) TYPE GE-

[1] This treatment of the Ebenaceae is the fourth contribution in a series of treatments of cultivated ligneous plants, the preparation of which is a project of the Arnold Arboretum of Harvard University, and the purpose of which is to provide a modern, accurate account of the woody plants encountered in cultivation in the cooler temperate regions of North America. It is hoped that these treatments will eventually form the basis of a new manual of cultivated woody plants. The first paper in this series was published in the Journal of the Arnold Arboretum **56**: 1–19. 1975. Reference should be made to the introductory paragraphs of that paper for matters concerning area covered, taxa included, and the general philosophy of these treatments.

Special thanks and gratitude are extended to the Director and trustees of the Stanley Smith Horticultural Trust for a grant that has made possible the illustrations to accompany these treatments. The illustrations are the careful work of Robin S. Lefberg and were prepared from living and alcohol-preserved specimens collected in the Arnold Arboretum and at the Henry Foundation for Botanical Research, Gladwyne, Pennsylvania.

For their contributions of time and advice and encouragement, I am indebted to my colleagues on the staff of the Arnold Arboretum and to many botanical and horticultural friends and colleagues. Particular thanks are extended to my wife, Harmony, to Dr. J. C. McDaniel, Mr. J. Witt, and Dr. B. G. Schubert. S. A. S.

NUS: *Ebenus* Burm. ex O. Kuntze = *Maba* J. R. & G. Forster = *Diospyros* L.

Upwards of 500 species in three to five genera distributed primarily in tropical and subtropical climates in both eastern and western hemispheres. Relatively few species are native in the Temperate Zone of North America and Asia; and other than species of *Diospyros* and *Lissocarpa* Bentham (two species of tropical South America), the genera of Ebenaceae are confined to Africa and Madagascar. *Diospyros* is the only genus with species both native to and cultivated in our area in North America.

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Diospyros Linnaeus, Sp. Pl. 2: 1057. 1753; Gen. Pl. ed. 5. 478. 1754.

Evergreen to deciduous trees and shrubs with very hard, often black wood; bark smooth, sometimes exfoliating, to deeply fissured and checkered; branchlets glabrous to densely pubescent, the pith continuous; winter buds (in ours) with 2 outer scales, these often persistent at the base of lateral shoots, terminal buds lacking. Leaves alternate, petiolate to subsessile, the membranaceous to coriaceous blades with entire, sometimes ciliate margins. Flowers staminate or carpellate (rarely perfect), and the plant dioecious, occasionally monoecious (or, due to the presence of occasional perfect flowers, the plants polygamous or polygamodioecious); staminate flowers 2–5 together, rarely solitary, short-pedicellate in short-pedunculate, bracteate, axillary cymose inflorescences; carpellate flowers usually solitary in the axils of leaves on short, bracteate pedicels. Calyx articulated at base, usually 4-lobed, occasionally 3–7-lobed, in carpellate flowers persistent, often accrescent. Corollas urceolate to ± campanulate, 3–7-, usually 4-lobed, the lobes spreading or recurved at anthesis. Stamens

usually 2 or 3 times the number of corolla lobes, free or occasionally in pairs, epipetalous in 2 or 3 whorls, the anther sacs linear-lanceolate, dehiscing by longitudinal slits; in carpellate flowers the androecium represented by staminodia or absent. Gynoecia absent or rudimentary in staminate flowers, in carpellate flowers the ovary superior, 3–16-, usually 8-locular, each locule with 1 or 2 ovules; styles usually 4, connate at least basally. Berries occasionally parthenocarpic and seedless, otherwise with seeds, depressed-globose, globose to oblong or conical, green through yellow to reddish-orange or brownish, blackish, or purplish when mature, often ± glaucous, the edible berries usually astringent prior to maturity due to high tannin content, becoming sweet and juicy with soft, pulpy flesh when ripe; seeds oblong to ± rounded, flattened, with ± shining, brown coats, the endosperm cartilaginous or sometimes ruminate. (Including *Maba* J. R. & G. Forster, *Brayodendron* Small.) LECTOTYPE SPECIES: *D. lotus* L., see N. L. Britton, N. Am. Trees 785. 1908. (Name from Greek, *Dios*, of Zeus or of Jove, and *pyros*, grain, in allusion to the sweet, edible fruits of the type species.) — PERSIMMON, DATE PLUM.

A taxonomically difficult genus of approximately 400 species of tropical to temperate climates in the Americas, Asia, and Africa. The greatest concentrations of species occur in Madagascar, from which over 100 species are known, in Malaysia, and in Africa. Relatively few species are known from the Temperate Zone, but two are native to the United States, and several are known from temperate Asia.

While several species from tropical and warm temperate areas are cultivated in California and Florida, only four species are documented as being cultivated in our area. Rehder (1940, 1949) included *Diospyros armata* Hemsley, Jour. Linn. Soc. London Bot. **26**: 69. 1889, and *D. sinensis* Hemsley, *Ibid.*: 71, both from China, in his *Manual* and *Bibliography*, but I have seen neither specimens from cultivation nor mention of their cultivation in North America; *D. armata* is, however, occasionally grown in gardens in England. Moreover, plants are grown within our region under the invalid name *D. duclouxii* Dode ex Pourtet (see under *D. lotus*).

The wood of several species of *Diospyros* is valued for lumber, and ebony, the wood of *D. ebenum* Koenig ex Retzius (see R. A. Howard & T. Norlindh, Jour. Arnold Arb. **43**: 94–102. *pls. 1–5.* 1962), is of considerable commercial value. The edible fruits of some species are also of importance as minor orchard crops, while the green, unripe fruits of *D. kaki* var. *silvestris* are used to make a waterproofing varnish oil in China (Wilson, 1913, p. 73). Numerous species of *Diospyros* are also considered to be of value medicinally, and throughout Asia numerous medicinal uses for different parts of the plants are known (personal communication, L. M. Perry). Still other species, particularly in the American tropics, are used as fish poisons.

The sexuality of individual plants and the production of fruit by species of *Diospyros* (particularly that of *D. kaki* and *D. virginiana*) in our area are variable and merit further investigation. Many carpellate plants fail

to hold and develop fruit to maturity due to the lack of staminate plants to insure pollination. Other plants, however, produce seedless fruits without pollination as the result of parthenocarpic development. Hume (1913) observed that, in addition to variability in fruit production, most plants of *D. kaki* produce either staminate or carpellate flowers, while occasional trees produce two or three types of flowers, viz. staminate, carpellate, and perfect. Some staminate trees produce perfect flowers (occasionally resulting in the development of fruits), and some carpellate plants either sporadically or regularly produce branchlets with staminate flowers and rarely a few perfect flowers (usually in association with the staminate flowers). Due to the scarcity of perfect flowers, they are not described in the descriptions that follow.

Hybrids between *Diospyros kaki*, *D. lotus*, and *D. virginiana* are mentioned by Grubov (1967), who states that these closely related species cross readily. J. C. McDaniel (personal communication), however, has informed me that interspecific hybridization in *Diospyros* appears to be considerably more difficult than in *Magnolia* (Magnoliaceae), and Morettini (1947) reported that he could not obtain interspecific hybrids between these three species. Reciprocal crosses between *D. kaki*, $2n = 90$, and plants of the hexaploid race, $2n = 90$, of *D. virginiana* have resulted in seed production when *D. virginiana* was used as the carpellate parent. However, the plants of the resulting F_1 generation "appear to have purely maternal inheritance . . ." (McDaniel, 1973). This evidence, together with the occasional parthenocarpic development of seedless (and seeded?) fruits suggests that some apomictic mechanism(s) may be present in *Diospyros*.

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KEY TO THE SPECIES OF DIOSPYROS IN CULTIVATION

1. Plants usually trees, rarely shrubs; leaf blades membranaceous to subcoriaceous, (1.4–)4–16(–20) cm. long, distinctly petiolate; flowers appearing after the leaves; anther sacs dehiscent by long, longitudinal slits; carpellate flowers with staminodia; fruits reddish through orange to yellow or yellowish-brown, sometimes purplish, rarely black. ..... 2.
2. Branchlets ± slender, glabrous or with grayish pubescence; staminate flowers 6–10 mm. long at anthesis; pedicels of carpellate flowers 2–7 mm. long, the corolla 5–12 mm. long; fruits to 4 cm. in diameter (very rarely larger). ..... 3.
3. Petioles (0.5–)1.8–3.2(–4.7) cm. long; staminate flowers 8–10 mm. long at anthesis; corolla of carpellate flowers ca. 12 mm. long, the 4 or 5 lobes 7–8 mm. long; mature berries reddish-orange to pinkish-yellow, rarely purplish or black, to 4 cm. (or rarely to 7.5 cm.) in diameter; seeds 11–17 mm. long. ..... 1. *D. virginiana.*
3. Petioles 0.7–1.2(–2) cm. long; staminate flowers 6–7 mm. long at anthesis; corolla of carpellate flowers ca. 5 mm. long, the 4 or 5 lobes 2–3 mm. long; mature berries yellowish-brown to bluish-black, to 2 cm. in diameter; seeds 8–12 mm. long. ..... 2. *D. lotus.*
2. Branchlets ± stout, variously fulvous-pubescent; staminate flowers 11–14 mm. long at anthesis; pedicels of carpellate flowers 8–32 mm. long, the corolla ca. 15 mm. long; fruits to 7.5 cm. in diameter. ..... 3. *D. kaki.*
1. Plants usually shrubs, rarely small trees; leaf blades coriaceous, (1.4–)2.4–4.8 cm. long, subsessile; flowers appearing with the expanding leaves in spring; anther sacs dehiscent by short, apical slits; carpellate flowers lacking staminodia; fruits black. ..... 4. *D. texana.*

1. D. virginiana Linnaeus, Sp. Pl. 2: 1057. 1753. FIGURE 1, a–h.

Irregularly branched deciduous trees, often with ± pendulous branches, to 10 or 15 m., rarely to 35 m., or occasionally shrubs, the plants often suckering from the roots; bark hard, brownish or blackish, irregularly and deeply fissured into small, blocklike plates; branchlets slender, greenish- to purplish-tan, lenticellate, finely to densely villous and/or glandular-pubescent, becoming glabrous in age and sometimes deciduous at 2 or 3

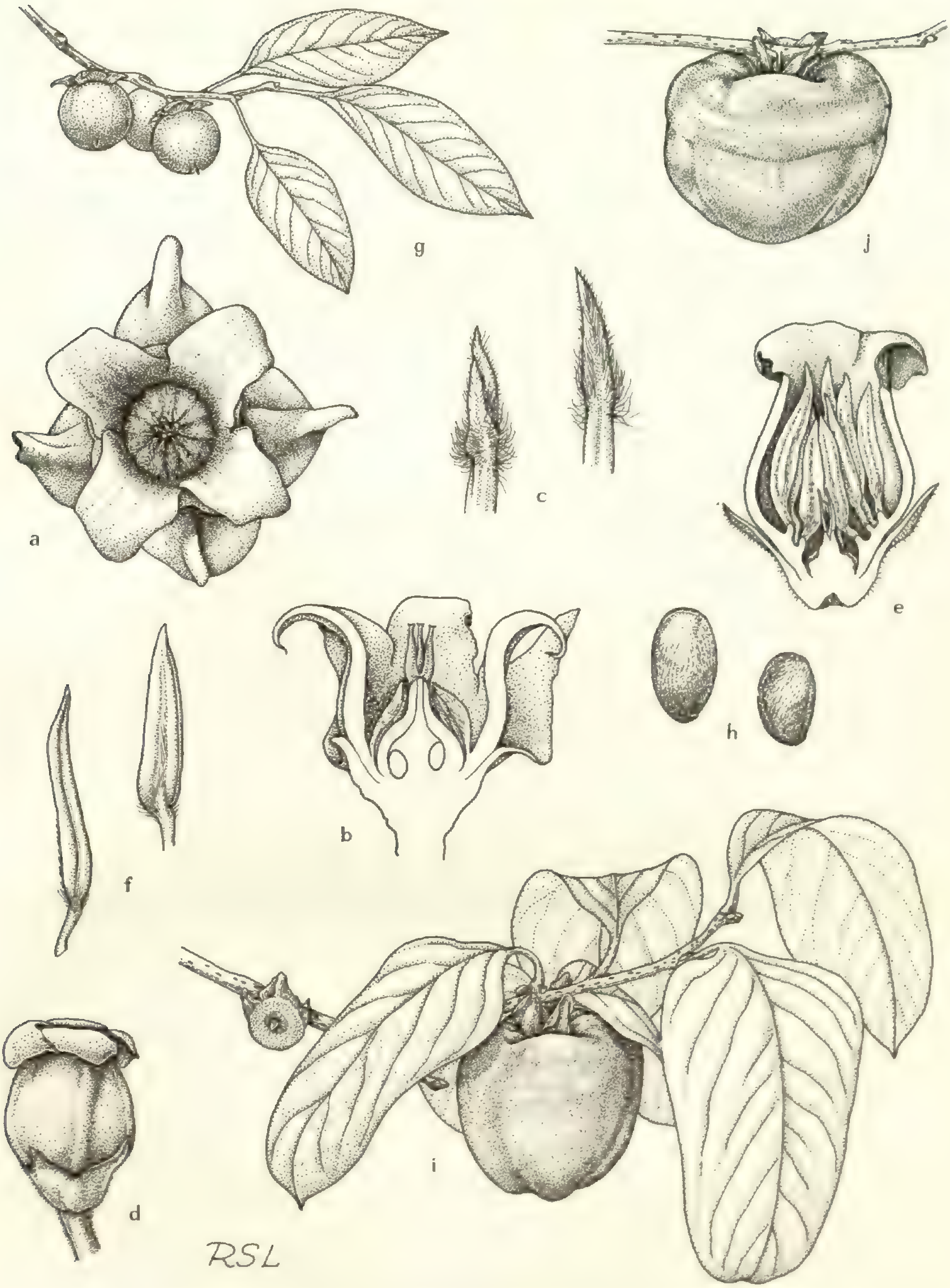

FIGURE 1. **Diospyros.** a–h, *D. virginiana*: a, carpellate flower showing foliaceous calyx lobes, recurved corolla lobes, and staminodia over the ovary, from above, × 3; b, longitudinal section of carpellate flower, × 3; c, two staminodia, × 6; d, staminate flower, × 3; e, longitudinal section of staminate flower showing epipetalous stamens and rudimentary gynoecium, × 4; f, functional stamens from staminate flower, × 6; g, habit of fruiting branchlet of carpellate plant, × ⅜; h, seeds, × 1. i, j, *D. kaki*: i, habit of fruiting branchlet of carpellate plant, × ⅜; j, fruit of the cultivar 'Tamopan', × ⅜.

years by abscission; winter buds small, 3–4 mm. long, ± pointed with 2 outer scales, the outermost scale overlapping the inner scale, both persistent at the base of lateral shoots. Leaves held ± drooping; petioles (0.5–)1.8–3.2(–4.7) cm. long, finely pubescent and glandular, particularly when young; leaf blades ± leathery, (2.9–)3.2–12(–20) cm. long, (1.4–)2–6.5(–8.4) cm. wide, elliptic to ovate or typically oblong with acute to acuminate apices, entire margins (ciliate when young, sometimes persistently), and obtuse to ± truncate or attenuate bases; upper surfaces of the blades dull to lustrous dark green, the midveins and major lateral veins pubescent and/or glandular, otherwise glabrous; lower surfaces pale grayish-green, glabrous or with long hairs scattered over the surface, in live material the venation finely reticulate, the ultimate veinlets darker than the areolae and prominent. Flowers produced on the current year's growth, held ± nodding beneath the leaves. Staminate flowers 8–10 mm. long at anthesis, short-pedicellate, 3 or 4 together (or fewer through abortion) in glandular-pubescent, short-pedunculate, bracteate, cymose inflorescences, the bracts caducous; calyces green, pubescent, the 4 (or 5) deltoid to linear lobes (2–)3–4 mm. long; corolla 8–10 mm. long, white, ± urceolate and strongly 4- (or 5-)ribbed, the lobes yellowish, recurved, ca. 3 mm. long; stamens 8–16, epipetalous in 1 or 2 whorls, the largest stamens ca. 7 mm. long; gynoecia rudimentary, seemingly nectar-secreting. Carpellate flowers solitary on short, glabrous or puberulent, bracteate, persistent pedicels 4–6(–7) mm. long; calyces foliaceous, 12–14 mm. long, green, densely silvery-pubescent on the adaxial surface of the calyx tube, accrescent in fruit and sometimes persistent on the branchlets, the 4 or 5 lobes folded downward along the median line, 9–10 mm. long at anthesis; corolla white, ± urceolate, ca. 12 mm. long, the lobes 7–8 mm. long, yellowish, recurved; staminodia 8, curved over the surface of the ovary, pubescent with long silvery hairs; ovary ± globose, glabrous, the 4 (or 5) styles pubescent, connate basally. Berries globose, depressed-globose, oblong, or conical, to 4 cm. in diameter, often remaining on the branchlets into winter, astringent when green, becoming sweet and orangish to pinkish-yellow, often with a grayish bloom when ripe, sometimes seedless due to parthenocarpy; seeds oblong, flattened, 11–17 mm. long, the seed coats tan to reddish-brown, ± shining. $2n = 60, 90$. — COMMON PERSIMMON, AMERICAN PERSIMMON, SIMMON, POSSUMWOOD.

Native to a wide area of the eastern United States from southern Connecticut and Long Island south to southern Florida and westward into eastern Iowa, Kansas, Oklahoma, and Texas. (See E. L. Little, Jr., Atlas of U. S. Trees 1: *map 123-E.* 1971, and H. A. Fowells, Silvics of Forest Trees of the U. S., *map*, p. 168. 1965).

Diospyros virginiana is a variable species, and several varieties and forms have been recognized. As is pointed out by Wood and Channell (1960) and reiterated by Steyermark (1963), the validity of some of these subspecific taxa, particularly var. *pubescens*, is questionable and should be considered tentative until a detailed analytic study of the variability of the

species is made. However, as Steyermark has stated (p. 1176), ". . . it would be unscientific at the present time, merely because of apparent intergradations and noncorrelations between the variations, to combine all variations into one highly variable taxon." As a consequence, and because these variants may be encountered in cultivation, they are described below.

Plants of *Diospyros virginiana* with villous or densely tomentose branchlets and with the lower surfaces of the mature leaves obviously pubescent can be referred to var. *pubescens* Nuttall, N. Am. Sylva 2: 46. 1846 (*D. pubescens* Pursh, *D. virginiana* var. *pubescens* (Pursh) Dippel). Plants of this taxon have been recorded as occurring sporadically within the range of var. *virginiana* from Florida west to Arkansas and northward into Virginia, southern Illinois, and southern Iowa. Shrubby plants 1–4 m. high (rarely small trees) with the leaf blades smaller (3–8 cm. long, 2–4 cm. wide) than leaves of var. *pubescens* have been recognized as *D. virginiana* f. *pumila* Palmer & Steyerm., Ann. Missouri Bot. Gard. 22: 616. 1935. These plants are of local distribution in Missouri and Arkansas.

Also of localized distribution on the western edge of the species range in Missouri and Kansas southward into Arkansas and Oklahoma, plants developing depressed-globose fruits up to 7.5 cm. in diameter that ripen early in the season (July to September) and which have leaf blades broadly rounded to subcordate at base have been distinguished as *Diospyros virgiana* var. *platycarpa* Sargent, Jour. Arnold Arb. 2: 168. 1921. Other variants that correspond to var. *platycarpa* but produce dark purplish or bluish fruits have been designated as *D. virginiana* f. *atra* Sarg., *Ibid.*: 170. Finally, shrubs or small trees of peninsular Florida that produce thick-skinned fruits with plump, somewhat rugose seeds have been segregated as *D. virginiana* var. *mosieri* (Small) Sarg., *Ibid.*: 170. (*D. mosieri* Small, Jour. N. Y. Bot. Gard. 22: 33. 1921).

During the late 19th and early 20th centuries, considerable interest centered around *Diospyros virginiana* as a potential orchard crop in the United States. Several cultivars, selected primarily for fruit color, taste, size, and earliness of maturation, were selected from wild populations and named. Lists and descriptions of many of these cultivars (most probably no longer available commercially) are to be found in Bailey (1902), Fletcher (1915), Troop and Hadley (1896) and Watts (1899). Interest in and selection of *D. virginiana* cultivars has continued to the present, primarily in the Midwest. Recently described cultivars are discussed by Brooks and Olmo (1972) and in several articles by J. C. McDaniel.

2. **D. lotus** Linnaeus, Sp. Pl. 2: 1057. 1753.

Small, deciduous trees with rounded crowns, in nature to ca. 26 m. (*fide* E. H. Wilson), in cultivation usually smaller; bark smooth, grayish, in age becoming rough and deeply fissured into small blocklike plates; branchlets slender, green, becoming reddish-brown or orange-brown, eventually light grayish- or silvery-tan, finely pubescent or glabrous, the periderm finely striated, lenticellate; winter buds small, 4–6 mm. long, with 2 outer

scales, the outermost scale overlapping the inner scale, both persistent at the base of lateral shoots. Petioles 0.7–1.2(–2) cm. long, glabrous or finely pubescent, often with orange glands; leaf blades membranaceous, (4.1–)5–15(–19) cm. long, (1.8–)3.5–5.8(–7.5) cm. wide, narrowly lanceolate or broadly elliptic to ovate or usually oblong with short-acuminate apices, entire margins (sparsely ciliate when young), and obtuse to attenuate bases; upper surfaces of the blades glossy dark green, glabrous or with hairs scattered along the midveins, rarely with hairs over the lamina; lower surfaces pale grayish-green usually sericeous or with hairs scattered over the lamina, sometimes glabrous, in live material the venation not appearing decidedly reticulate, the ultimate veinlets not prominent. Flowers produced on the current year's growth, held ± nodding beneath the leaves. Staminate flowers 6–7 mm. long at anthesis, short-pedicellate, 3–5 together (or fewer through abortion) in rufous-pubescent, short-pedunculate, bracteate, cymose inflorescences, the bracts caducous; calyces green, finely pubescent, the 4 (or 5) deltoid lobes 1.5–2 mm. long; corolla 4.5–6 mm. long, white, ± campanulate and weakly 4- (or 5-)ribbed, the lobes pinkish or yellowish, recurved, ca. 2 mm. long; stamens 16, rarely fewer, epipetalous in 2 whorls, the largest stamens ca. 4 mm. long; gynoecia abortive or rudimentary. Carpellate flowers solitary on short, pubescent, bracteate pedicels 2–3 mm. long; calyces green, 7–8 mm. long, densely rufous-pubescent on the adaxial surface of the calyx tube, accrescent in fruit and sometimes persistent on the branchlets, the 4 or 5 lobes foliaceous, 6–7 mm. long at anthesis; corolla reddish-brown, broadly urceolate, ca. 5 mm. long, the lobes 2–3 mm. long, ± recurved; staminodia 8, curved over the surface of the ovary, pubescent with long, silvery hairs; ovary ± globose, glabrous or pubescent at apex, the 4 (or 5) styles glabrous or finely pubescent, connate basally. Berries globose to ovoid, up to 2 cm. in diameter, astringent when green, becoming yellowish-brown to bluish-black, often with a waxy bloom, and sweet when ripe; seeds oblong, flattened, 8–12 mm. long, the seed coats brown, $2n = 30$. (*D. lotus* var. *typica* Makino; including *D. japonica* Siebold & Zuccarini, *D. lotus* var. *japonica* (Sieb. & Zucc.) Franchet, *D. kaki* var. *glabra* A. DC., *D. lotus* var. *glabra* (A. DC.) Makino, *D. duclouxii* Dode ex Pourtet.) — DATE PLUM.

Cultivated since ancient times; judged to be native to a wide area from Asia Minor and the Caucasus through Afghanistan, the northwestern Himalayan region, and into China. Widely cultivated in the Mediterranean area where the plants are valued for their sweet, datelike fruits, *Diospyros lotus* has become naturalized in the Balkan Peninsula and in other areas of southern Europe; it is also cultivated throughout most of China and Japan, both for its fruits and as a rootstock onto which scions of *D. kaki* are grafted.

Makino (Tokyo Bot. Mag. 26: 396, 397. 1912) has recognized three forms of *Diospyros lotus* based on fruit shape. *Diospyros lotus* f. GLOBOSA, with globose fruits, is listed as the wild type, while f. OVOIDEA, fruits ovoid, and f. ELLIPSOIDEA, fruits ellipsoid, are known from cultivation. I have

not seen these variations in cultivation in our area, but it is likely that they should be treated as cultivars, much as similar variations in the fruits of *D. kaki* have been treated.

Diospyros duclouxii Dode ex Pourtet, Ann. École Nat. Eaux & For. 9: 576. 1949 (an invalid name lacking a Latin description), included here tentatively in the synonymy of *D. lotus*, was described briefly and attributed to Dode by Pourtet. Plants are grown under this name in several botanical gardens and arboreta in the United States and Europe, but based on the few specimens that I have seen, it would appear that the plants are variants of *D. lotus*. Pourtet states (translation mine), "Asia: China. This species appears quite distinct: the acuminate leaves remain pubescent on the upper surface and the young bark fissures into small, squarish platelets similar to those of *D. virginiana*." These characters, however, seem insufficient to distinguish the plants as a different taxon.

3. **D. kaki** Linnaeus f., Suppl Pl. 439. 1781. FIGURE 1, i & j.

Moderate-sized, deciduous trees to ca. 14 m., usually with rounded crowns, or rarely large shrubs; bark pale gray, scaly, sometimes exfoliating in irregular patches, or, in grafted cultivated plants, the bark usually grayish or brownish and furrowed; branchlets ± stout, brownish-gray or reddish- to orange-brown, variously fulvous-pubescent, eventually glabrous and lenticellate; winter buds small, 4–5 mm. long, ovoid to subglobose, usually pubescent, with 2 outer scales, the outermost scale overlapping the inner one, both persistent at the base of lateral shoots. Leaves held ± drooping, becoming reddish-orange in fall; petioles (0.5–)1–2.2(–3) cm. long, sparingly to densely pubescent; leaf blades variable in size and shape, ± subcoriaceous, (5–)6.5–16(–20) cm. long, 3–8.8 (–11) cm. wide, ovate to oblong-ovate, broadly elliptic, obovate, or sometimes suborbicular, with truncate or rounded to cuneate bases, entire margins, and obtuse, acute, or (usually) acuminate apices; upper surfaces of the blades dark, glossy green, glabrous or with hairs along the veins and sometimes scattered over the surface; lower surfaces paler green, variable in indumentum, usually fulvous-villous along the veins and often sparingly pubescent over the surface, the midveins and 5 or 6 pairs of lateral veins prominent, elevated, the lower lateral veins ending high on the blade. Flowers produced on the current year's growth, held ± nodding beneath the leaves. Staminate flowers 11–14 mm. long at anthesis, short-pedicellate, 3–5 together (or fewer through abortion) in fulvous-pubescent, short-pedunculate, bracteate cymose inflorescences, the bracts caducous; calyces green, glabrous or sparingly pubescent, the 4 ovate to deltoid lobes 3–7 mm. long; corolla 10–13 mm. long, light yellow, ± campanulate to ± urceolate, the 4 lobes recurved, ca. 5 mm. long; stamens 16–24, epipetalous in 2 or 3 whorls, the largest stamens ca. 8 mm. long; gynoecia abortive or rudimentary. Carpellate flowers solitary on pubescent, bracteate pedicels (8–)14–20(–32) mm. long in the axils of leaves; calyces green, densely rufous- or fulvous-pubescent on the adaxial and abaxial sur-

faces of the calyx tube, 15–22 mm. long, accrescent in fruit and sometimes persistent on the branchlets, the 4 lobes foliaceous, 15–17 mm. long at anthesis; corolla yellowish, broadly urceolate, ca. 15 mm. long, the 4 lobes 6–8 mm. long at anthesis with ciliate margins, ± recurved; staminodia 8, curved over the surface of the ovary, pubescent with long, silvery hairs; ovary depressed-globose, globose, or conical, glabrous, the 4 styles pubescent, connate basally. Berries to 7.5 cm. in diameter, variable in shape, globose or depressed-globose to oblong or conical, sometimes with longitudinal furrows and occasionally with a ± hemispherical or basal constriction, astringent when green (or some cultivars sweet when hard and green), becoming sweet, and yellow through orange to reddish when ripe, sometimes seedless due to parthenocarpy; seeds variable in size and shape, broadly to narrowly oblong, flattened, 1–3 cm. long, the seed coats dark brown. $2n = 90$. (*D. chinensis* Blume, *D. kaki* var. *domestica* Makino; including *D. roxburghii* Carrière, *D. lycopersicon* Carrière.) — KAKI, JAPANESE PERSIMMON, CHINESE PERSIMMON, ORIENTAL PERSIMMON, PERSIMMON.

An exceedingly variable species (sometimes divided into several species) widely cultivated throughout China and Japan where a myriad of cultivars has been developed, selected, and grown since remote antiquity; also grown in regions of temperate and warm temperate climates throughout the world. In our area *Diospyros kaki* is known to be hardy as far north as the Philadelphia region, and it is also grown successfully in Massachusetts on Martha's Vineyard.

Diospyros kaki var. *silvestris* Makino, Tokyo Bot. Mag. 22: 159. 1908, oil-persimmon, is the reputed wild plant from which the kakis in cultivation have been derived, but it should be noted that Hume (1914) has suggested that the cultivated kakis are of hybrid origin and have two or more species in their genetic background. According to Rehder and Wilson (1916, p. 590), plants of var. *silvestris* occur as escapes from cultivation in Japan and China, and Wilson (1913, p. 73) reports that it is "abundant in the mountains of central and western China up to 4000 feet altitude, where it forms a large tree 50 or 60 feet tall." Grubov (1967), however, has suggested that the wild progenitor of the cultivated forms was originally native to northern China where it was an element of the deciduous forest vegetation.

Specimens of *Diospyros kaki* var. *silvestris* that I have seen are extremely variable, and some are difficult if not impossible to distinguish from specimens of var. *kaki*, to which the above description applies. The majority of specimens of var. *silvestris* have smaller leaf blades (generally about 10.5 cm. long and 4.5 cm. wide), densely fulvous-pubescent branchlets and petioles, and smaller flowers, the carpellate ones often with pubescent ovaries. The fruits generally contain seeds, are golden yellow at maturity, and are mostly smaller (1.5–5 cm. in diameter) than those of var. *kaki*. While I have not seen specimens documenting its occurrence as a cultivated plant in this country, it might be expected in some arboretum collections.

Moreover, plants grown from seed of var. *kaki* might be expected to represent reversions to this wild type.

Among the possibly more than 1000 horticultural forms of *Diospyros kaki* var. *kaki*, Rehder (1940, 1949) accounted for 'Costata' (= *D. kaki* var. *costata* (Carrière) André, *D. costata* Carrière), a cultivar that produces large, orange-red, depressed-globose fruits with four longitudinal furrows, and 'Mazelii' (= *D. kaki* var. *mazelii* (Carrière) Mouillefert, *D. mazelii* Carrière), a variant producing large orange-yellow fruits with eight longitudinal furrows. Other notable cultivars include 'Tamopan' (see F. N. Meyer, 1911), which produces large, seedless, ± depressed-globose, ± four-sided reddish-orange fruits with an equatorial or ± basal constriction (FIGURE 1, j); and 'Hachiya', the cultivar probably most commonly seen in produce markets. The fruits of 'Hachiya' are oblong-conical, with glossy deep orange-red skin, and deep yellow flesh which remains astringent until soft. 'Gailey' is another important cultivar inasmuch as it is planted for its dependable production of some staminate flowers on otherwise carpellate individuals. These staminate flowers provide a source of pollen for pollination of other cultivars. For information and descriptions of many other cultivars of *D. kaki*, reference should be made to Gould (1940), Condit (1919), Ryerson and Hodgson (1933), Brooks and Olmo (1972), and Bailey (1902).

Apparently, most of the cultivars of the kaki produce fruit through parthenocarpic development, but the production of fruit is often erratic when pollination and fertilization are not insured. Hume (1913, 1914) found that fruit production was assured on a regular basis if carpellate trees that regularly produce some branchlets with staminate flowers are included in orchard plantings. He classed the cultivar 'Gailey' as a "staminate constant" due to its regular abundant production of staminate flowers, while 'Hachiya' and 'Tamopan', among others, were termed "pistillate constants," since they have never been observed to produce staminate flowers.

Hume also noted that in some clones the color of the flesh of the mature fruits is the same regardless of parthenocarpic development or development following pollination and fertilization. In other clones the flesh color of fruits developing after pollination and fertilization is darker than the flesh of parthenocarpic fruits of the same clone. On the basis of this reaction (or non-reaction), Hume placed several cultivars into two groups, viz. pollination constants, clones which undergo no color changes as a result of pollination, and pollination variants, clones in which flesh color of mature fruits is darker if developed from pollinated and fertilized flowers. This informal classification is mentioned here since some nurseries and commercial growers employ it when selling and discussing named cultivars.

4. **D. texana** Scheele, Linnaea 22: 145. 1849.

Twiggy, deciduous shrubs or small trees, rarely to 16 m.; bark of older limbs smooth, light reddish-gray or reddish-brown, the outer layers exfo-

liating in irregular sheets, exposing the smooth, gray, inner bark; branchlets slender, silvery-gray, at first densely hirsute, eventually glabrous; winter buds very small, densely pubescent. Leaves sometimes persistent into winter, subsessile, the petioles 0.5–3 mm. long; leaf blades coriaceous, (1.4–)2.4–4.8 cm. long, (0.6–)1.3–2.2 cm. wide, obovate to oblong-obovate, with rounded, ± truncate, or sometimes shallowly emarginate apices, entire revolute margins, and cuneate bases; upper surfaces of the blades dark lustrous green, usually finely hirtellous; lower surfaces paler green, reticulate, hirsute. Flowers appearing in spring with the expanding leaves, produced on the current year's growth. Staminate flowers 7–8 mm. long at anthesis, borne on slender, hirtellous, bracteate pedicels, solitary or usually 2 or 3 together in short-pedunculate, cymose inflorescences; calyx green, divided almost to the base into 5 (or 6) pubescent, oblong to ovate lobes, the lobes ca. 3 mm. long; corolla 7–8 mm. long, creamy white, ± campanulate with 4 or 5 short, spreading to recurved lobes, the lobes sericeous on the abaxial surfaces; stamens usually 16, rarely fewer, epipetalous in 1 or 2 whorls, glabrous, the linear-lanceolate anther sacs apically dehiscent by short slits; gynoecia abortive or vestigial. Carpellate flowers solitary (rarely 2 together) on stout, bracteate, hispid pedicels ca. 4 mm. long; calyces 6–7 mm. long, divided almost to the base into 5 oblong, pubescent lobes, the lobes ca. 6 mm. long; corolla creamy white or greenish, broadly urceolate to ± campanulate, ca. 8 mm. long, the 5 lobes ca. 4 mm. long, spreading to recurved, rounded; stamens and/or staminodia lacking; ovary globose to ovoid, densely pubescent, the 4 glabrous styles connate at base and coherent for most of their length. Berries shining black and sweet at maturity, subglobose or depressed-globose, finely pubescent, 1.2–2.5 cm. in diameter, subtended by the accrescent calyx; seeds ± oblong, ca. 11 mm. long, the seed coats grayish-black with a ± metallic luster. $2n = 30$. (*Brayodendron texanum* (Scheele) Small.) — BLACK PERSIMMON, MEXICAN PERSIMMON, CHAPOTE.

Endemic to central and western Texas and northern Mexico in the states of Coahuila, Nuevo Leon, and Tamaulipas. Although it is rarely cultivated, we have evidence that *Diospyros texana* is included in the collections at Longwood Gardens and at Colonial Williamsburg, Virginia.

As pointed out by Sargent (1894), this species should prove valuable in cultivation for its attractive, lustrous foliage, the interesting black fruits of carpellate plants, and its mottled bark resembling that of the crapemyrtle (*Lagerstroemia indica* L., Lythraceae). Standley (1924, p. 1127) notes, however, that the fruits of *Diospyros texana* leave "an indelible black stain upon everything with which [they] come in contact . . ."

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THE NAJADACEAE IN THE SOUTHEASTERN UNITED STATES[1]

ROBERT R. HAYNES

NAJADACEAE A. L. de Jussieu, Gen. Pl. 18. 1789, "Naiades," nom. cons.
(NAIAD FAMILY)

A monogeneric family of herbaceous submersed monocotyledons distinguished by subopposite serrulate leaves; axillary imperfect flowers, the staminate each consisting of one stamen and the ovulate each consisting of a single 1-ovuled gynoecium with a solitary, basal, anatropous ovule.

The Najadaceae are of somewhat uncertain taxonomic position. Some workers, e.g., Cronquist and Lawrence, have considered the family to be closely related to the Potamogetonaceae. Miki, however, suggested that it may be derived from the Hydrocharitaceae. The Najadaceae have been considered to consist of one genus, *Najas*, by Cronquist and Lawrence; four genera, *Najas*, *Potamogeton*, *Ruppia*, and *Zannichellia*, by Fassett and Eyles & Robertson; and five genera, *Najas*, *Potamogeton*, *Ruppia*, *Zannichellia*, and *Zostera*, by Gleason (in Gleason & Cronquist). After a recent study of the floral development of *Najas flexilis*, Posluszny & Sattler stated that it is advisable to keep the Najadaceae as a monogeneric family and to place it along with the Potamogetonaceae and Zannichelliaceae in one order. Their views are followed here.

1. Najas Linnaeus, Sp. Pl. 2: 1015. 1753; Gen. Pl. ed. 5. 445. 1754.

Plants glabrous, herbaceous, annual or rarely perennial, growing submersed in fresh or brackish waters, monoecious or dioecious. Stems slender, much branched, rooting at the lower nodes, sometimes armed with spinulose teeth on the internodes. Leaves subopposite or appearing whorled due to reduced internode length, sessile, each divided into blade and sheath; blade linear and flattened, 1-nerved, sometimes abaxially toothed on the

[1] Prepared for the Generic Flora of the Southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation. This treatment follows the format established in the first paper in the series (Jour. Arnold Arb. 39: 296–346. 1958). The area covered includes North Carolina, South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions apply primarily to the plants of this area, with supplementary information in brackets. References that I have not seen are marked by an asterisk.

The illustration was drawn by Karen S. Velmure under my direction from material collected by Ronald L. Stuckey in Ohio and by C. Barre Hellquist in Massachusetts.

I am indebted to Dr. Carroll E. Wood, Jr., principal investigator on the project, for his advice, suggestions, and help with the literature during the preparation of the manuscript.

midrib, the margins usually serrulate with 5–100 teeth per side, the apex acute to acuminate, with 1–3 teeth per side, the teeth multicellular, formed by layers of cells decreasing in cell number distally and terminated by a large, sharp-tipped cell, or unicellular; sheaths variously shaped, each inclosing a pair of tiny hyaline scales, the margins usually spiny-toothed with 1–8[–15] teeth per side. Flowers imperfect, axillary, sessile or short pedunculate, solitary or clustered; perianth absent. Staminate flowers subtended by one or two clear to pale purple membranaceous envelopes [these rarely absent], each flower consisting of a single stamen; pedicel at first short, elongating at anthesis, pushing the anther through the outer envelope; anther sessile, 1- or 4-locular, dehiscing irregularly; pollen 3-celled, globose or ellipsoid, densely filled with starch, monocolpate, the wall with shallow reticulations, thin, not divided into exine and intine. Ovulate flowers sessile, an envelope absent [rarely present]; gynoecium ending in a short style with 3 or 4 branches; ovary 1-loculate, the wall delicate, 2 cell layers thick; ovule solitary, basal, anatropous, 2-integumented. Fruit 1-seeded, the gynoecial wall 2 cells thick, closely enveloping the seed, which is released by decay of the wall. Seeds fusiform, the seed coat hard, brittle, 3- or several-cell-layered, areolate; areolae formed by two outer cell layers of the seed coat, irregularly arranged or in 15–40 [–50] rows, variously rectangularly shaped, the end walls often raised giving the seed coat a papillose appearance; endosperm absent; embryo elongate, without lateral enlargement of the cotyledon. TYPE SPECIES: *N. marina* L. (Name Greek and Latin, *Naias*, a water-nymph, a Naiad.) — BUSHY PONDWEED, NAIAD, WATER-NYMPH.

A nearly cosmopolitan genus of perhaps 40 species, divided into 2 subgenera, NAJAS, with only one species, and CAULINIA. Rendle divided subgenus CAULINIA into four sections based upon the presence or absence of the floral envelopes. In an investigation of the Asiatic and Malaysian species, De Wilde determined the presence of the envelopes to be too inconsistent to distinguish sections. The view of De Wilde is here accepted, and no sections are recognized. The genus is represented in the United States by eight species, at least some of which are widely distributed; six of them occur in our area.

Subgenus NAJAS (plants dioecious, seed coat several cell layers thick, internodes and abaxial surface of leaf blade spiny), represented by *N. marina*, is widespread in warm areas of the world, from Europe and Africa east to Japan, the Malaysian region, and Australia, and in North, Central, and South America. *Najas marina* L. (including *N. gracilis* (Morong) Small, *N. major* All.), spiny naiad, $2n = 12$, is a variable species occurring in the United States from North and South Dakota, Minnesota, Wisconsin, Michigan, Ohio, and New York, to Florida, Texas, Arizona, Utah, Nevada, and California. The species is found mostly in brackish or highly alkaline waters. It has been divided into numerous varieties based on minor differences in the size of leaves and the number of spines on the internodes. Such variations usually can be found within single populations and,

therefore, do not warrant taxonomic recognition. Viinikka, however, has observed two cytological races of the species, one with B chromosomes and one lacking them. He has indicated (pers. comm.) that these races correspond to differences in morphology. Specimens with large seeds and leaves (no size given) invariably lack accessory chromosomes, whereas plants with smaller seeds and leaves possess B chromosomes. He has not yet decided on appropriate categories for these apparent entities.

Subgenus CAULINIA (Willd.) Ascherson (Fl. Prov. Brandenburg 1: 670. 1864) (plants monoecious, testa three cell layers thick, internodes and abaxial surface of leaf blade spineless) consists of about 40 species, most of which occur in the Eastern Hemisphere. Five species are represented in our area. *Najas ancistrocarpa* Magnus (including *N. conferta* of authors) has a disjunct distribution in southeastern Asia and in the southeastern United States, where it is known from Leon and Santa Rosa counties, Florida, and from Decatur County, Georgia. The species is easily recognized by its crescent-shaped seeds with areolae longer than broad. *Najas Wrightiana* A. Br. is restricted in the United States to Collier County, Florida. It is easily separated from other species of *Najas* by its short (1–1.5 mm.), erect seeds with 5-angled areolae, the large teeth scattered along the margins of quite narrow leaves, and its bushy appearance produced by axillary tufts of leaves and very short internodes.

Najas minor All., $2n = 12$, is an Old World species that apparently invaded North America about 50 years ago. According to Meriläinen, it thrives in eutrophic waters and can tolerate pollution. With the gradual eutrophication of the waters of the eastern United States, the plant has spread from New York to Illinois, south to Florida, Mississippi, and Arkansas. *Najas minor* can be determined easily by its mature recurved leaves and by its seeds with areolae broader than long. The seeds are occasionally slightly curved but not as much as those of *N. ancistrocarpa*. *Najas minor* displays a seasonal dimorphism. Wentz & Stuckey have shown that young individuals have leaves erect to ascending, and not until late in the growing season does the characteristic recurved pattern develop. *Najas gracillima* (A. Br.) Magnus occurs in the United States from New Hampshire to Alabama, west to Minnesota and Missouri, and in California. The species can be distinguished by the style arising excentrically at the apex of the gynoecial wall. Apparently intolerant of pollution, the plant has become exceedingly rare in some areas of the eastern United States.

Najas guadalupensis (Sprengel) Magnus is widely distributed throughout the country, except in the Rocky Mountain States. It can be distinguished from other North American species by seeds 1.2–2.5 mm. long, with (4- or) 6-angled areolae, and leaves with small, unicellular teeth. It is one of the many highly variable aquatic species, and has, therefore, been divided into several specific and infraspecific taxa. Clausen (1936), Oosstroom, and Wentz & Haynes have discussed variability within this species and have suggested that it should probably be treated as several closely related taxa. Haynes & Wentz later recognized two varieties, both of which occur within our area. Varietas *guadalupensis* occurs throughout

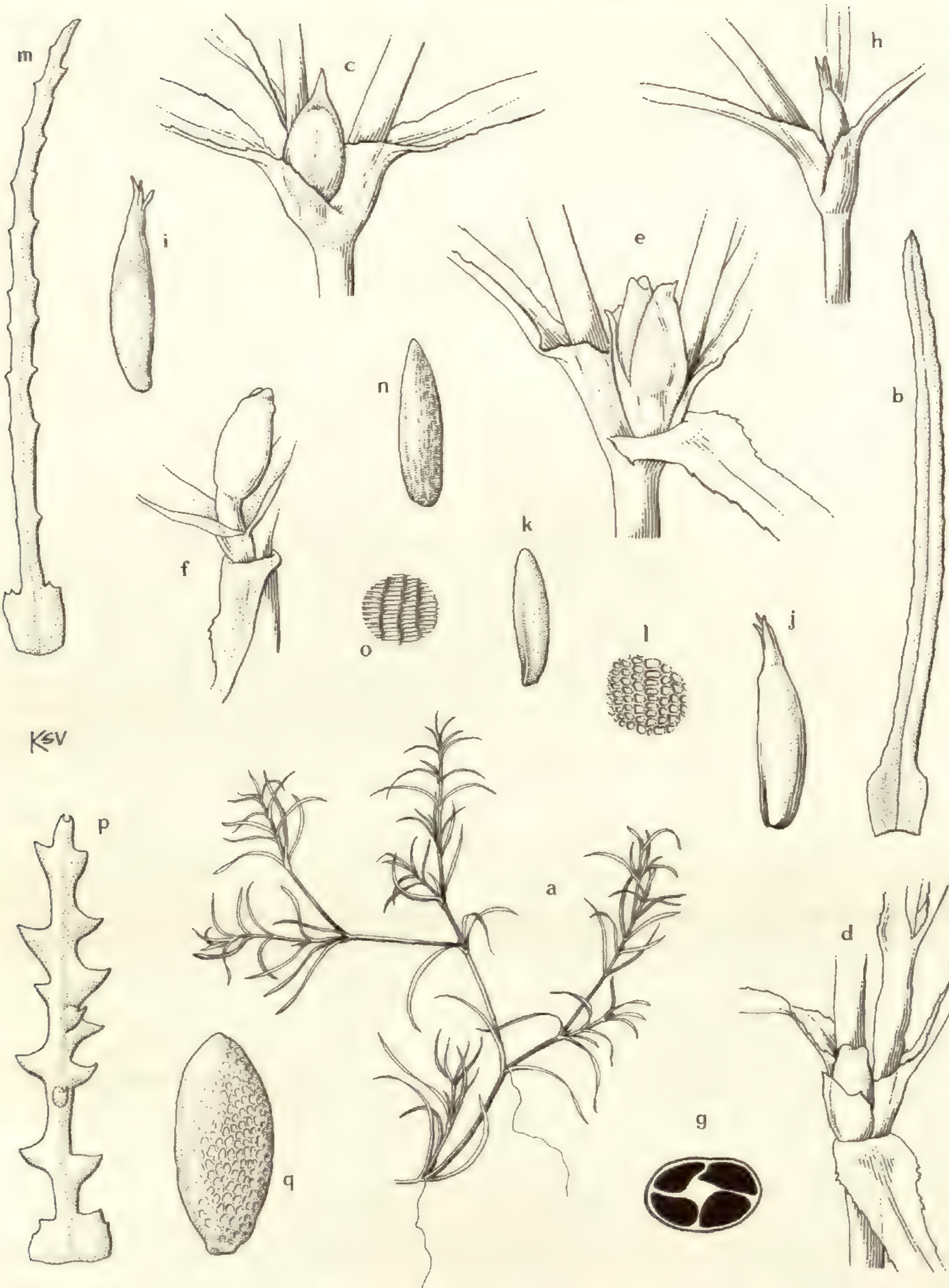

FIGURE 1. **Najas.** a–l, *N. guadalupensis*: a, habit of plant × ½; b, leaf, adaxial side, × 5; c, young staminate flower, the outer envelope intact, × 6; d, later stage, the outer envelope ruptured, stamen inclosed in inner envelope (two-lobed at tip), × 6; e, staminate flower at anthesis, pollen shed through opening between two lobes of inner envelope, × 6; f, still later stage, the outer envelope pulled back to show pedicel of staminate flower, × 6; g, diagrammatic cross section of anther to show four locules, × 12; h, carpellate flower, × 6; i, carpellate flower, ovule showing through ovary wall, × 10; j, fruit, × 10; k, seed, × 10; l, detail of seed coat, showing areolae, × 25. m–o, *N. minor*: m, leaf, adaxial side, × 5; n, seed, × 10; o, detail of seed coat, × 25. p, q, *N. marina*: p, leaf, abaxial side, × 3; q, seed, × 10.

the southeastern United States, while var. *floridana* Haynes & Wentz is restricted to Florida, southeastern Georgia, and Alabama. The varieties can be distinguished by the length of the seeds (var. *guadalupensis* 1.2–1.5 mm., and var. *floridana* 1.6–2.2 mm.).

The characters of the seeds of *Najas* are the most important ones for distinguishing the various taxa of the genus. Among the most distinctive characters are the arrangement of the areolae, either irregular (*N. marina*) or in rows (all other North American species of *Najas*); the shape of the areolae, longer than broad (*N. ancistrocarpa, N. marina, N. gracillima*) or broader than long (*N. minor, N. guadalupensis*), and 5-angled (*N. Wrightiana*); the length of the seeds; and the shape of the seeds, crescent-shaped (*N. ancistrocarpa*), fusiform (*N. gracillima, N. guadalupensis, N. Wrightiana*), slightly recurved (*N. minor*), or ovoid (*N. marina*). Of lesser importance for identification are the teeth along the margins of the leaf blades. These may be inconspicuous and composed of one large cell or conspicuous and formed of layers of cells decreasing in number outward and terminated by a large, sharp-tipped cell. Because of the importance of the seeds for the identification of *Najas*, care should be taken to collect seed-bearing specimens.

Sculthorpe has provided a review of the floral morphology of *Najas* which is controversial. The origin and significance of the floral envelopes have been of particular concern (see Miki, Rendle, and De Wilde). Posluszny & Sattler recently examined the floral development of *N. flexilis*, and their interpretations are presented here. Both staminate and ovulate flowers are produced terminally on an axillary shoot and, shortly after initiation, produce girdling primordia about their peripheries. In the staminate flower, the girdling primordium develops into an outer envelope two cell layers thick. Toward maturity, the distal portion of the outer envelope becomes elongated and stylelike, often with two or three branches. As the outer envelope is developing, a second girdling primordium is initiated which develops into the inner envelope. The inner envelope becomes closely appressed to the developing anther and is eventually almost indistinguishable from it except for its slightly protruding bilobed tip. The staminate flower develops a short stalk which usually elongates at anthesis.

The primordium of the ovulate flower develops into a two-cell-layered gynoecial wall which, near maturity, becomes elongated into a three- or four-lobed style. The floral apex is transformed into an ovule primordium as the apex is overgrown by the gynoecial wall. Two integuments are initiated, after which the ovule turns down, eventually becoming anatropous.

Posluszny & Sattler conclude that, since the ovule primordium is initiated in an exactly terminal position (a transformed floral apex) and not laterally on the gynoecial appendage, the carpel concept cannot be applied to the genus. According to them, the gynoecium of *Najas* is clearly acarpellate. They do not speculate whether this condition is primitive or derived.

Chase examined eight species of *Najas* and found that in all except *N.*

marina the seed coat is composed of three layers, with the inner layer somewhat membranaceous and compressed and the middle and outer layers quite stony. The outer layer, however, was observed to slough partly away in many species, this resulting in the pitting of the areolae of the testa. The outer layer does not slough away in species with a smooth seed coat, whereas some sloughing occurs in those with a rough one.

The genus is economically important in two respects. As a source of food for waterfowl, Martin & Uhler rank it eighth in importance in the United States and Canada, and Gaevskaya lists 18 species of animals that have been known to feed on it. In addition, populations of *Najas* have often been abundant enough in the southeastern United States to be regarded as weeds warranting the use of various methods of control.

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A REVISION OF THE GENUS ACRADENIA (RUTACEAE)*

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THE AUSTRALIAN GENUS *Acradenia* Kippist is known to occur naturally from the Macpherson Range on the Queensland–New South Wales border, south, discontinuously, to western Tasmania (see MAP 1).

Since its discovery in the mid-1800's, *Acradenia* has almost universally been considered to consist of a single species, *A. frankliniae*, endemic to Tasmania. Only Mueller (1868 and 1868a) suggested otherwise when he observed that the eastern Australian *Bosistoa sapindiformis* (correctly known as *B. pentacocca*, the type species of *Bosistoa*) might be better placed in *Acradenia*, and proposed for it the name *Acradenia bosistoi*. This idea was not accepted by subsequent authors, and, indeed, Mueller had erred. *Bosistoa pentacocca* has multi-ovulate carpels and buds with scales, and is clearly not congeneric with *Acradenia frankliniae*.

I have found, however, that *Bosistoa euodiiformis*, described by Mueller from northeastern New South Wales in 1875, *is* congeneric with *Acradenia frankliniae*, and that the sole species of the genus *Luerssenidendron* Domin, *L. monostylis*, is conspecific with *Bosistoa euodiiformis*. The purpose of this paper is to revise *Acradenia* in view of this new information.

Acradenia is distinguishable from all known genera of Rutaceae in the Australasian–Malesian region by the following combination of characters: leaves opposite, flowers 5-merous, stamens twice the number of the petals, carpels each with two ovules, and fruits follicular. The prominent carpellary glands of *Acradenia* are also distinctive, although similar structures are found in at least two other genera of Australasian-Malesian Rutaceae, namely, *Flindersia* and *Pentaceras*.

As might be expected, considering its relict-like geographic distribution, *Acradenia* does not have any particularly close generic affinities. *Bosistoa*, *Medicosma*, and *Zieria* are perhaps the most similar of the Australasian–Malesian Rutaceae, but they are obviously not close relatives of *Acradenia*. The need for caution in accepting the traditional classification of the Rutaceae is evident here, as it was in my study of *Acronychia* (Hartley, 1974). Although *Acradenia* was placed along with about 20 other genera in the tribe Boronieae by both Bentham (1863) and Engler (1896 and 1931), it is equally, if not more closely, related to several genera placed by those authors in the tribe Zanthoxyleae. It is worth noting that a Chilean genus, *Pitavia*, has carpellary glands that are remarkably similar to those of *Acradenia*, but it differs in having indehiscent fruits and 4-merous flowers.

This study is based on herbarium specimens. The contributing herbaria (with abbreviations, where available, from Holmgren & Keuken's *Index Herbariorum*, ed. 6. Part I. Regnum Vegetabile. p. 92. 1974) are as fol-

* This is the ninth in a series of papers on the Rutaceae of Malesia and Australasia.

MAP 1. Distribution of the genus *Acradenia*: *A. euodiiformis* (F. Muell.) Hartley (dots) and *A. frankliniae* Kippist (triangles).

lows: Arnold Arboretum of Harvard University, Cambridge (A); State Herbarium of South Australia, Adelaide (AD); British Museum (Natural History), London (BM); Queensland Herbarium, Brisbane (BRI); Botanical Survey of India, Calcutta (CAL); C.S.I.R.O. Herbarium Australiense, Canberra (CANB); Botany Division, Department of Scientific and Industrial Research, Christchurch (CHR); New South Wales Forestry Commission, Coffs Harbour (COFFS HARBOUR); Gray Herbarium of Harvard University, Cambridge (GH); The University of Tasmania, Hobart (HO); Royal Botanic Gardens, Kew (K); Rijksherbarium, Leiden (L); National Herbarium of Victoria, Melbourne (MEL); National Herbarium of New South Wales, Sydney (NSW); New York Botanical Garden, New York (NY); Muséum National d'Histoire Naturelle, Paris (P); Herbarium of the University of California, Berkeley (UC); National Museum of Natural History (Department of Botany), Smithsonian Institution, Washington, D. C. (US); and Naturhistorisches Museum, Wien (W). I wish to thank the directors and curators of these herbaria for making specimens in their care available to me.

Acradenia Kippist, Proc. Linn. Soc. London 2: 201. 1853; Trans. Linn. Soc. London 21: 208. 1854. TYPE SPECIES: *Acradenia frankliniae* Kippist.

Luerssenidendron Domin, Bibliot. Bot. 22(89): 289. 1927. TYPE SPECIES: *Luerssenidendron monostylis* Domin.

Shrubs or trees; indumentum of simple trichomes; buds naked. Leaves opposite, digitately trifoliolate, pinnately veined, with pellucid, punctate or pustular oil glands. Inflorescences paniculate, subcorymbose. Flowers bisexual; sepals 5 (rarely 6), basally connate, valvate, persistent in fruit; petals 5 (rarely 6), distinct, imbricate, plane (neither hoodlike nor apically hooked), deciduous in fruit; stamens twice the number of the petals, the antesepalous about as long as the petals, the antepetalous slightly shorter, filaments straight, sublinear, tapering to a subulate apex, anthers 2-celled, dehiscing by longitudinal slits, versatile, broadly elliptic, bluntly mucronulate; disc intrastaminal, pulvinate to columnar, usually angled between the filaments; gynoecium 5- (rarely 4-) carpellate, carpels basally connate and joined adaxially at about the middle by a single style, otherwise contiguous, each with a prominent upper abaxial gland, 1-locular, placentation upper axile, the placenta toward the apex of and protruding into the locule, ovules collateral, 2 per locule, style straight, twisted, about twice the length of the carpels, stigma scarcely differentiated. Fruit of 1–5 basally connate, 1-seeded follicles, undeveloped carpels, if any, persistent; follicles erect, obovate-truncate, transversely ribbed, dehiscent along the apical and adaxial edges; epicarp (the two outer layers of the pericarp — the exocarp and the mesocarp) dry at maturity, subwoody; endocarp cartilaginous, discharged (probably forcibly) with the seed. Seed narrowly to broadly and obliquely pyriform; testa brown, smooth, polished, pergamentaceous; endosperm fleshy, scant; embryo straight, obo-

vate, cotyledons plano-convex, emarginate at the point of attachment of the hypocotyl, hypocotyl terminal, subglobose.

The two species of *Acradenia*, while unquestionably distinct, are nevertheless very closely related, their only significant differences being vegetative. In view of their geographically discontinuous, eastern Australian–Tasmanian distribution (MAP 1) and their ecological preference for temperate rain forests, it seems likely that they have descended from a more widely distributed Tertiary population.

During the Tertiary there was land connection between Tasmania and the Australian mainland, and, up through the Eocene, climatic conditions were such that temperate rain forests were more widespread than in subsequent times. In the middle and late Tertiary there was a general climatic shift, from mild and humid conditions to a drier and cooler climate, by the onset of the Pleistocene. This brought about contraction and fragmentation of the Australian temperate rain forest areas, and may have produced geographic isolation that led to speciation in *Acradenia*.

Speciation may, however, have occurred at a later date. During the Pleistocene in Australia, there were at least two periods when there was broad land connection between Tasmania and the mainland, and an unknown number (at least three or four) of alternating wet and dry periods. These climatic oscillations almost certainly caused expansions and contractions of temperate rain forest areas in southeastern Australia. If one of these expansions was great enough, and also coincided with a suitable Tasmanian–mainland connection, then there may have existed a continuous population of *Acradenia* between Tasmania and southeastern Queensland. Speciation might then have occurred after this continuous population became discontinuous. (In the above discussion, data regarding events of the Tertiary and Pleistocene were obtained largely from Australian biogeographical studies which include summaries of the geological literature, for example, Burbidge (1960), Keast (1961), and Rawlinson (1974).)

An alternative explanation for the origin of these species is that the geographic isolation that led to speciation was the result of long-distance dispersal. This is not a likely possibility, however, because the wingless seeds of *Acradenia* clearly have no adaptation for dissemination of more than a few hundred meters. Another point against long-distance dispersal as a possible explanation is given below.

Further evidence concerning the origin of the two species of *Acradenia* comes from the study of two other pairs of vicarious species of Australian plants whose ranges and ecological preferences are closely homologous with those of *Acradenia*. These are the two Australian species of evergreen *Nothofagus*, *N. cunninghamii* (Hook. f.) Oersted and *N. moorei* (F. Muell.) Krasser,[1] and the two species of the genus *Anopterus* (Escalloniaceae), *A. glandulosus* Labill. and *A. macleayanus* F. Muell. The distribu-

[1] The only other species of *Nothofagus* in Australia, *N. gunnii* (Hook. f.) Oersted, an endemic of alpine regions of Tasmania, is deciduous and has a different type of pollen from that found in the two evergreen species (*cf.* van Steenis, 1971).

tional data given below for the species of *Anopterus* and *Nothofagus* were obtained from Bauer (1957), Curtis (1956 and 1967), Francis (1970), Fraser & Vickery (1938), R. D. Hoogland (personal communication), Moore (1893), and Willis (1973).

Nothofagus cunninghamii occurs in both Tasmania, where it is characteristic of temperate rain forests, and south central Victoria, where it usually lives in wet sclerophyll forests. *Nothofagus moorei* is known only from mountain rain forests from the Barrington Tops Plateau, New South Wales (about 40 miles north of the Hunter River, which is the southern boundary of the range of *Acradenia euodiiformis*), north to the Macpherson Range. Thus, with the exception of the Victorian population of the former, *Nothofagus cunninghamii* and *N. moorei* have about the same geographic distributions, respectively, as *Acradenia frankliniae* and *A. euodiiformis*.

Anopterus glandulosus is endemic to Tasmania, where it occurs in wet sclerophyll forests and temperate rain forests. *Anopterus macleayanus* is restricted in its distribution to rain forest habitats from Port Macquarie, New South Wales, north to the Macpherson Range. Thus, the distributions of these two species closely match those of *Acradenia frankliniae* and *A. euodiiformis*.

It is evident, as van Steenis (1971) has pointed out, that *Nothofagus* is not adapted for long-distance dispersal. Also, the fossil record provides ample evidence that *N. cunninghamii* and *N. moorei* are relicts. *Anopterus*, on the other hand, is obviously well adapted for wind dissemination, having light-weight, winged seeds. In spite of this, I do not think that long-distance dispersal provides the correct explanation for the origin of its two geographically disjunct species. The distance between their two areas (about 800 miles) is not particularly great by long-distance dispersal standards, and it seems that if such dispersal and establishment happened once, it would have happened several times, thus preventing speciation by the repeated introduction of the original genotype.

The geographical and ecological similarities between these species of *Nothofagus*, *Anopterus*, and *Acradenia* may be interpreted as evidence that their two groups of vicarious species (*Nothofagus moorei*, *Anopterus macleayanus*, and *Acradenia euodiiformis* in the north; *Nothofagus cunninghamii*, *Anopterus glandulosus*, and *Acradenia frankliniae* in the south) are relict assemblages, and that the three genera have been together for a very long period of time during which geographic isolation and speciation occurred. *Nothofagus* pollen of the *menziesii* type, found in *N. cunninghamii* and *N. moorei*, is known from several Tertiary deposits (Eocene to Pliocene) ranging from northeastern New South Wales to southern Victoria (*cf.* Cookson, 1946), so it is likely that the *Nothofagus-Anopterus-Acradenia* assemblage dates back to that period.

The possibility that the two modern species of *Acradenia* are each part of a relict assemblage of similarly vicarious species considerably strengthens the case against long-distance dispersal.

I have found no evidence that one of the species of *Acradenia* is more

primitive than the other, so they are arranged alphabetically in the following taxonomic section.

KEY TO THE SPECIES

1. Rather small to large tree; branchlets smooth; petiole 1–7.5 cm. long; leaflets 4–23 cm. long; inflorescences 6–21 cm. long. . . . . 1. *A. euodiiformis.*
1. Shrub or small tree; branchlets pustular-glandular; petiole 0.3–0.8 cm. long; leaflets 2–6 cm. long; inflorescences 2–5 cm. long. . . . . 2. *A. frankliniae.*

1. **Acradenia euodiiformis** (F. Muell.) Hartley, comb. nov.

FIGURE 1.

Bosistoa euodiiformis F. Muell. Frag. Phytogr. Austral. **9**: 174. 1875 (as "*euodiformis*"). TYPE: *Wilcox*, New South Wales, upper Clarence River.
Luerssenidendron monostylis Domin, Bibliot. Bot. **22**(89): 289. *t. 29.* 1927. TYPE: *Moore*, New South Wales, head of Hastings River.

Rather small to large tree to about 30 m.; branchlets pubescent when very young, becoming glabrous, neither glandular nor glaucous. Leaves pustular-glandular and often sparsely puberulent when very young, becoming punctate and entirely glabrous; petiole 1–7.5 cm. long; leaflets

FIGURE 1. *Acradenia euodiiformis* (F. Muell.) Hartley. Flowering branchlet (drawn from *Jones 13*), × ⅓.

narrowly elliptic to oblanceolate, 4–23 cm. long, 1.2–6.5 cm. wide, base cuneate to attenuate, midrib evident but usually not prominent, main veins visible but usually faint, 8–12 on either side of the midrib, margin entire or, less often, crenate toward the apex, apex obtuse to acute or occasionally acuminate. Inflorescences from the axils of the upper leaves, several- to many-flowered, 6–21 cm. long; peduncle, upper axis, and branches sparsely puberulent to glabrate; pedicels sparsely puberulent to glabrate, slender, 4–12 mm. long. Flowers 6–6.5 mm. long; sepals green, 5, sparsely pubescent abaxially, ciliate on the margin, triangular, 1–1.5 mm. long; petals white to cream, 5, tomentose abaxially, sparsely pubescent adaxially, elliptic to narrowly obovate, 5.5–6 mm. long; stamens with glabrous filaments, anthers 1.5 mm. long; disc glabrous, 0.5–0.8 mm. high; carpels 5, tomentose except for the glabrous, upper abaxial gland, 1.5–2 mm. high; style glabrous. Follicles tomentose, 6–8 mm. high; endocarp glabrous. Seed about 5 mm. long.

ILLUSTRATION. Domin, K. *loc. cit.* (as *Luerssenidendron monostylis*).

DISTRIBUTION. Macpherson Range, southeastern Queensland, south to the Hunter River, New South Wales; rain forests to 1200 meters. See MAP 1.

Queensland. MORETON DISTRICT. Macpherson Range: 0.4 km. beyond turnoff to Picnic Rock, West Canungra Creek, *Smith 11290* (BRI); road to Moran's Falls, near Lamington National Park, *Smith 14187* (BRI); Moran's Creek Paddock, Lamington Plateau, *Whaite 3032* (NSW); upper Coomera River, Balnamboolah Falls, *Perry 507* (CANB); Roberts Plateau, *O'Reilly*, September, 1929 (BRI), *White*, January, 1919 (BRI); Lamington National Park, near Mt. Hobwee, *White 6172* (A, BRI, NY, UC), *6172A* (A, BRI); Lamington National Park, O'Reilly's Guest House, *Smith*, December, 1963 (BRI), *Smith & Webb 3641* (BRI), *Webb 5008* (CANB); Lamington National Park, *Moore 54* (BRI), *Tryon & White*, March, 1920 (A, NSW, P), *White & Tryon*, March, 1920 (BRI); Springbrook, *Rudder 4018* (BM, K), September 6, 1929 (BRI), September, 1930 (A). **New South Wales.** Whian Whian State Forest, *Constable*, January 15, 1953 (L, NSW 22341, US), *Hayes*, January, 1953 (COFFS HARBOUR), *Jones 13* (BRI), *351* (BRI), *951* (CANB), October, 1966 (BRI), *Moriarty 703* (BRI, CANB), *1689* (CANB), *1690* (CANB), *Webb & Tracey*, 1953–1958 (BRI, CANB), July, 1956 (BRI); Bangalow, *Baeuerlen*, December, 1896 (NSW 128875); Tintenbar, *Baeuerlen 590* (NSW), September, 1893 (NSW 128877); upper Clarence River, *Wilcox*, November, 1875 (MEL, holotype of *Bosistoa euodiiformis* F. Muell.); Clarence River, *Beckler* (MEL); Chapmans Plains, *Hayes & McGillivray*, October 27, 1966 (COFFS HARBOUR); Dorrigo State Forest, *Davis*, October 15, 1955 (AD), *White 7562* (A, BRI, NY); Dorrigo, *Boorman*, March, 1909 (NSW 128879), September, 1909 (NSW 128880), *Fraser*, January 23, 1934 (NSW 128881), *Vickery*, April 15, 1953 (NSW 128882); Mobong Creek, *Hayes*, October 29, 1953 (COFFS HARBOUR); Bruxner Park, *Anonymous*, October 16, 1952 (COFFS HARBOUR), *Schodde & Hayes 3532* (A, CANB); about 25 miles W of Urunga, *Hayes & McGillivray 2508* (NSW); upper Taylors Arm, *Hayes*, August 15, 1952 (COFFS HARBOUR); McLeay River, *Anonymous*, 1895 (MEL), *McDonald*, 1894 (MEL); head of Hastings River, *Moore* (K, holotype of *Luerssenidendron monostylis* Domin; GH, isotype); 5 miles SE of Yarrowitch, *Johnson*, October 19, 1953 (NSW 128883); upper Myall

River, *Rupp*, September 29, 1924 (NSW 128888); Doyles River Road about 48 miles W of Wauchope, *Garden*, October 6, 1951 (NSW); Mt. Boss State Forest, South Branch of Wilson River 15 miles NW of Wauchope, *Constable*, October 31, 1956 (NSW 128884); Port Macquarie, *Anonymous*, July, 1891 (NSW 128885); Doyles River State Forest, 30 miles NW of Taree, *Constable 6317* (BRI, NSW); Dingo State Forest, 15 miles W of Wingham, *Schodde 5117* (CANB); Bo Bo Creek, *Jones*, June, 1946 (COFFS HARBOUR); Comboyne, *Chisholm*, November, 1923 (NSW 128887); Ellenborough Falls, *Maiden & Boorman*, October, 1902 (NSW 135709, W); upper Allyn River, *Floyd*, October 31, 1972 (COFFS HARBOUR); Booral, *Rudder*, October 30, 1892 (NSW 128889); Hunter River, *Rudder 3* (MEL).

There is no doubt that *Luerssenidendron monostylis* and *Bosistoa euodiiformis* are conspecific. It is surprising that Domin did not recognize this, because he saw material of the latter species. (However, the type of *L. monostylis* was in flower, while material of *B. euodiiformis* lacked flowers.) Instead, he tried to relate *L. monostylis* to *Pagetia monostylis* F. M. Bailey, stating that on the basis of Bailey's description and illustration (Queensl. Dept. Agr. Bot. Bull. No. 13. 7. 1895; Queensl. Fl. 1: 203. 1899; Comprehensive Cat. Queensl. Pl. 80. *t. 61*. 1909), the two appeared to be identical. They are not, and Domin may have suspected this since he designated a different type for *L. monostylis* and gave no indication that he intended to make a new combination.

2. **Acradenia frankliniae** Kippist, Proc. Linn. Soc. London 2: 201. 1853; Trans. Linn. Soc. London 21: 208. *t. 22*. 1854. TYPE: *Milligan 1038*, April, 1842, western Tasmania, Franklin River.

FIGURE 2.

Erect shrub or small tree to about 7 m.; branchlets sparsely to densely puberulent, pustular-glandular, usually becoming glaucous. Leaves pustular-glandular; petiole densely puberulent to glabrous, 0.3–0.8 cm. long; leaflets with scattered appressed hairs above and below or glabrous throughout, narrowly elliptic to oblanceolate, 2–6 cm. long, 0.5–2 cm. wide, base cuneate, midrib prominent, lateral veins not visible, margin entire toward the base, crenate toward the apex, apex rounded to obtuse. Inflorescences terminal or terminal and from the axils of the upper leaves, few- to several-flowered, 2–5 cm. long; peduncle covered with rather coarse, appressed hairs, upper axis and branches sparsely puberulent to glabrous; pedicels sparsely puberulent to glabrous, slender, 5–10 mm. long. Flowers 5–7 mm. long; sepals green, 5 (in occasional flowers, 6), sparsely pubescent abaxially, ciliate on the margin, ovate to broadly elliptic, 1–1.5 mm. long; petals white, 5 (in occasional flowers, 6), tomentose abaxially and adaxially in bud, becoming sparsely pubescent, broadly elliptic, 4.5–6 mm. long; stamens with glabrous filaments, anthers 1–1.2 mm. long; disc glabrous, about 0.5 mm. high; carpels 5 (in occasional flowers, 4), tomentose except for the glabrous, upper abaxial gland, about 1 mm. high; style glabrous. Follicles tomentose, 6–8 mm. high; endocarp sparsely hairy on the inner surface. Seed about 5 mm. long.

FIGURE 2. *Acradenia frankliniae* Kippist. Flowering branchlet (drawn from *Milligan 727*, November 6, 1846), × ⅔.

ILLUSTRATIONS. Curtis's Bot. Mag. **153**: *t. 9187*. 1927. Kippist, R. *loc. cit*. Rodway, L. Tasmanian Fl. opp. pg. 22. 1903. Stones, M. and W. M. Curtis, The endemic flora of Tasmania. Part 5. *t. 167*. 1975.

DISTRIBUTION. Pieman River south to the Gordon and Franklin Rivers in the vicinity of Macquarie Harbour, western Tasmania; stream margins in temperate rain forests at lower elevations. See MAP 1.

Tasmania. Pieman River at Corinna, *Jackson 258* (HO), *Olsen*, January 14, 1941 (HO); Pieman River, *Gilbert*, February, 1947 (HO), *Simson 1735* (MEL); Macquarie Harbour at Brisbanes Bay, *Milligan 727*, August 17, 1846 (MEL), *727*, November 6, 1846 (GH, NY), *727*, November 15, 1846 (MEL), *727*, March 9, 1847 (K); Macquarie Harbour, *Milligan 727*, October 6, 1846 (K, W), *727* (GH, K, MEL, NY, P), *without number or date* (A, CAL); road to Macquarie Harbour, *Milligan 1038*, 1842 (HO); King River, *Somerville*, April 22, 1947 (HO); Gordon River, banks of Big Creek 8 miles from the mouth, *Milligan 727*, October 12, 1846 (K); Gordon River, *Anonymous*, November 24–27, 1937 (HO), *Olsen*, December 13, 1946 (HO), *Somerville*, January, 1949 (HO); Franklin River, *Atkinson*, November, 1932 (HO), *Milligan 1038*, April, 1842 (K, holotype), *1038*, February 8, 1845 (K); without definite locality, *Anonymous*, February 3, 1867 (MEL). CULTIVATED. **New Zealand.** New Plymouth, *Sykes 918/62* (CHR).

EXCLUDED NAME

Acradenia bosistoi F. Muell. Pap. Proc. Roy. Soc. Tasmania **8**: 8. 1868, and Frag. Phytogr. Austral. **6**: 167. 1868, *nomen illegit*. (*in obs.* and based on *Euodia pentacocca* F. Muell.) = **Bosistoa pentacocca** (F. Muell.) Baill.

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SINORADLKOFERA: A NEW GENUS OF SAPINDACEAE

FREDERICK G. MEYER

IN 1900, HEMSLEY published *Koelreuteria minor*, describing it as a small sapindaceous tree from the province of Kwangtung, China. Hemsley noted that "no flowers have yet been received, but it is so very distinct that we do not hesitate to describe the otherwise complete specimens." The description of the 13 foot high tree was based upon a single collection with mature capsules. It may be noted that, lacking flowers, Hemsley's original figure of *K. minor* included the foveolate, strophiolate seeds, which are unlike the smooth, stipitate seeds of *Koelreuteria*. The lack of flowers in all the available specimens caused Radlkofer (1933) and all subsequent authors to place the plant in the genus *Koelreuteria*. How and Ho (1955) cited a specimen with flowers (*Hwang, Ho, & Chia 130216*) from Lin-Kwei Hsien, Kwangsi, as a flowering specimen of *K. minor*, without recognizing that it was different from *Koelreuteria*. More recently, the plant continues to be listed as *K. minor* in a new flora of the People's Republic of China (Anonymous, 1972).

RELATIONSHIPS OF THE NEW GENUS

A single specimen (*Wang*) *Sun Yatsen University 40934* (A) with flowers at anthesis and in bud, provided the critical material for a detailed comparison of *Sinoradlkofera* with members of the genus *Koelreuteria*. The two genera are compared in TABLE 1.

The new genus is provisionally placed in subfamily Dyssapindaceae (Sapindaceae anomospermae) in the tribe Koelreuterieae (Radlkofer, 1931), near *Koelreuteria*. The strophiolate seeds, sessile disc, pubescent corolla lobes with rudimentary appendages, and geniculate stamens are characters that clearly distinguish the new genus from the previously established genera of the tribe Koelreuterieae.

The pollen of *Sinoradlkofera minor* is closely related to that of *Koelreuteria* (Meyer, 1976). Only the shape of the grains in the two taxa differs: prolate in *S. minor*, and more or less spheroidal in *Koelreuteria*. Although *K. elegans* (Seem.) A. C. Smith has a striate-reticulate ektexine, the two remaining species, *K. bipinnata* Franchet and *K. paniculata* Laxm., have an ektexine with mostly parallel striae, which closely resembles that of *Sinoradlkofera*.

KEY TO THE GENERA OF KOELREUTERIEAE

A. Trees with compound leaves with a naked rachis; sepals valvate.
  B. Flowers yellow, asymmetric; disc elevated on a short androgynophore; seeds stipitate, the surface smooth. China, Taiwan, Fiji. . . *Koelreuteria*.

TABLE 1

Sinoradlkofera	Koelreuteria
Leaflets 2.9–4.7 cm. long.	Leaflets 4.8–14.1 cm. long.
Main lateral branches of the inflorescence 5-branched.	Main lateral branches of the inflorescence 4-branched.
Flowers subregular, white.	Flowers asymmetrical, yellow.
Disc sessile, androgynophore absent.	Disc elevated on a short androgynophore.
Petals puberulent.	Petals glabrous.
Limb of petal straight, appendages absent or forming a narrow marginal flap.	Limb of petal reflexed, appendages well developed.
Stamens geniculate in bud.	Stamens straight in bud.
Pollen prolate.	Pollen more or less spheroidal.
Capsules obovoid, retuse.	Capsules tapering toward the apex, or rotund to suborbicular.
Seeds strophiolate, ca. 4 mm. in diameter, the surface usually foveolate, without a waxlike coating.	Seeds stipitate (funiculus persistent), 5–7 mm. in diameter, the surface smooth, often with a whitish, waxlike coating.

B. Flowers white, subregular; disc sessile; seeds strophiolate, the surface usually foveolate. Southern China. ..... *Sinoradlkofera.*

A. Shrubs with simple leaves, or leaves compound, rachis winged; sepals imbricate.

C. Thorny shrubs with simple leaves; capsule membranous, loculicidal, regulary dehiscent. Afghanistan and Pakistan. ..... *Stocksia.*

C. Unarmed shrubs with pinnate leaves and a winged rachis; capsule leathery-membranous, finally irregularly dehiscent. South Africa and Madagascar. ..... *Erythrophysa.*

Sinoradlkofera F. G. Meyer, gen. nov.

Inflorescentia paniculata; flores polygami, surregulares, albi; sepala valvata, adpresse puberulenta; petala versus basem disci sessilis inserta (androgynophorum nullum), unguiculata, ungue brevissime, limbo elliptico usque obovato, recto, puberulento, appendicibus carentibus vel rudimentalibus; stamina in alabastro geniculata, sub anthesi recta; antherae antrorsae, versatiles, glabrae; polline prolato; ovaria triloculares; capsulae retusae; seminae strophiolatae, saepe foveolatae.

SPECIES TYPICA: *Sinoradlkofera minor* (Hemsley) F. G. Meyer.

The name of the new genus, *Sinoradlkofera* (the prefix Sino = Chinese, the name *Radlkofera* having been preempted earlier for an African genus), is dedicated to Ludwig Adolph Timotheus Radlkofer (1829–1927), whose

FIGURE 1. *Sinoradlkofera minor*: a, habit of the plant, × ¼, from (*Wang*) *Sun Yatsen University 41208*; b, staminate flower, × 3; c, geniculate stamen, × 5; d, inflated retuse capsule showing persistent calyx, × ¾; e, staminate flower (petals missing), showing calyx, disc, pistil, and stamens at anthesis, × 3; f, pistillate flower (petals missing), showing aborted stamens, × 4; g, petal, × 8 (b–g from (*Wang*) *Sun Yatsen University 40934*); h, capsule with exposed seed, × ¾ (after Hooker's Ic. Pl. **XXVII:** *pl. 2642*; i, strophiolate seed, × 3 (*Tsang 28000*).

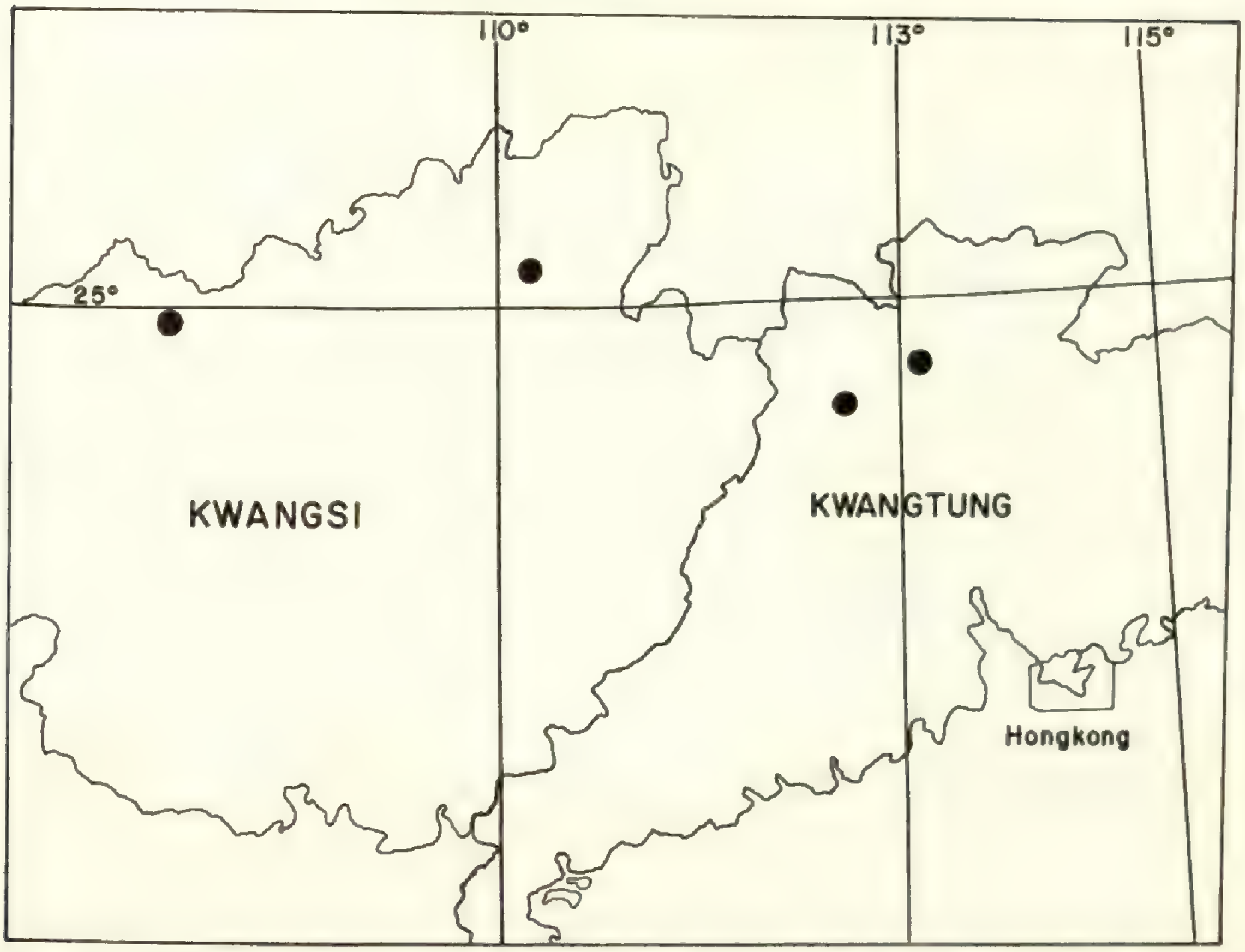


FIGURE 2. Distribution map of *Sinoradlkofera minor* in the People's Republic of China. According to How and Ho (1955), the distribution extends to the adjacent provinces of Hunan and Kweichow.

monumental world monograph of Sapindaceae (1931–1934) still remains the standard reference on this large and important family of flowering plants.

Sinoradlkofera minor (Hemsley) F. G. Meyer, comb. nov.

FIGURES 1, 2,[1] 3, 4.

Koelreuteria minor Hemsley, in Hooker, Ic. Pl. **XXVII:** *pl. 2642.* 1900; M. Smith in Forbes & Hemsley, Jour. Linn. Soc. Bot. **36:** 487. 1904; Dunn & Tutcher, Kew Bull. Add. Ser. **10:** 66. 1912; Chung, Mem. Sci. Soc. China **1**(1): 152. 1924; Radlkofer in Engler, Pflanzenr. **IV. 165:** 1332. 1933; Chun, Sunyatsenia **4:** 239. 1940; How & Ho, Acta Phytotax. Sinica **3:** 404. 1955; Anon., Icon. Cormophytorum Sinicorum **2:** 724. 1972. HOLOTYPE: China. Prov. Kwangtung, Lienchow River, 25 Aug. 1887, *Ford 291* (K!); isotypes (HK, K!).

Deciduous tree, to 20 m. tall; d.b.h. to 40 cm.; twigs and young branches smooth, dark brown, puberulent; lenticels superficial, roundish to lenticular, pale brown; pith white to brownish; axillary buds densely sericeous. Leaves alternate, once pinnate, 8–14 cm. long, 3–8 cm. wide;

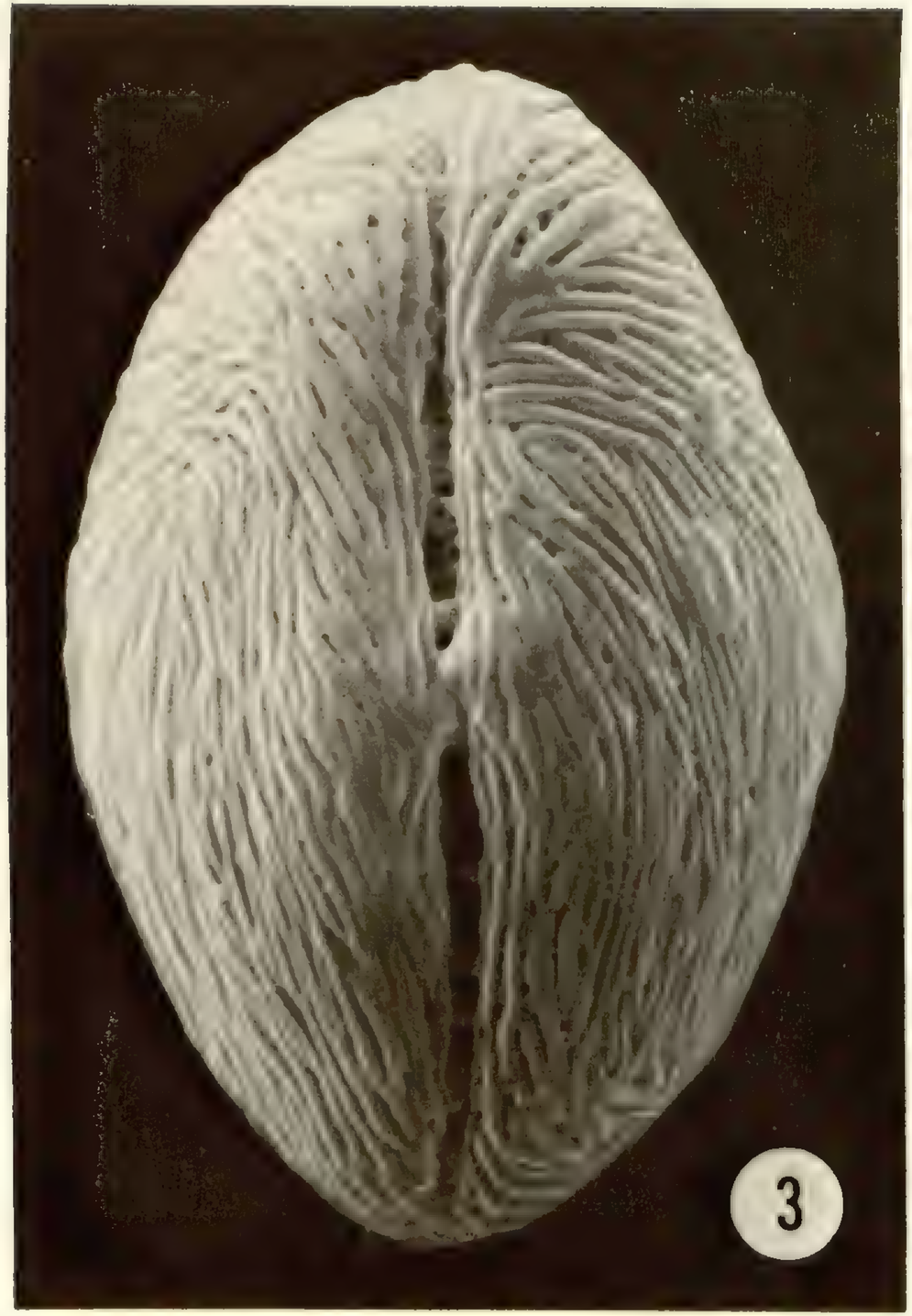
[1] The localities pinpointed on the dot map are in accordance with the *Mainland China, Gazetteer No. 22,* ed. 2, vols. 1 & 2. Prepared by the Geographic Names Division, Army Map Service, Washington, D. C. 1968.

petiole somewhat pulvinate at the base, the rachis densely puberulent; leaflets 10–17, alternate or rarely opposite, the blade elliptic, oblique on the posterior side, 2.9–4.7 cm. long, 1.2–1.4 cm. wide, shallowly crenate-serrate, with forward pointing teeth, thick membranous, lustrous above, lighter beneath, glabrous except for occasional tufts of hair in the marginal sinuses and with short straight hairs on the midvein above and below, rarely with minute reddish glands on the midvein above, the petiolule very short and densely puberulent. Inflorescence terminal, paniculate, pyramidal, much-branched, 12–19 cm. long, 10–15 cm. wide, the branches very slender, uniformly puberulent; flowers polygamous, small, subregular, the bracteoles caducous, the pedicels 2.5–3 mm. long; calyx lobes 5, valvate, persistent, 1.5–2.5 mm. long, ca. 1 mm. wide, 2 long (2.5 mm.) and 3 short (1.5 mm.), oblong to obovate, obtuse at the apex, uniformly densely appressed-puberulent on the outer face, less so on the inner face, often densely fringed with hairs on the margin; disc sessile, tumid; corolla inserted on the outer side of the disc, the petals unguiculate, elliptic to obovate, white, 2.8–3.0 mm. long, obtuse at the tip, the limb straight, puberulent, narrowed to the short claw at the base, appendages absent or forming a narrow marginal flap near the base; stamens 8, inserted on the disc at the base of the ovary, the filaments geniculate in bud, becoming straight at anthesis, ca. 4 mm. long, very short and abortive in the carpellate flowers, the anthers antrorse, versatile, smooth; ovary densely sericeous while young, 3-locular; placentation parietal, the ovules 6, 2 in each locule, more or less median, anatropous, 3 descending and the raphe dorsal, 3 ascending and the raphe ventral; stigmas 3. Capsules inflated, 3-locular, loculicidal, triangular in cross section, obovoid, 1.7–2 cm. long and 1.7–2 cm. wide, the valves winglike, papyraceous, roseate while young, rotund to suborbicular, retuse at the apex, glabrous or often minutely puberulent on the dorsal suture, with reticulate venation outside, lustrous within, the style persistent, ca. 0.7 mm. long; seeds 3, ca. 4 mm. in diameter, nearly spherical, hard, black, shiny, reddish scurfy on the hilum, strophiolate, usually foveolate, exalbuminous, the embryo spirally convolute.

POLLEN. Grains single, prolate, 23–26 μm. P $\times$ 14–15 μm. E, 3-colporate, the exine ca. 1.5 μm. thick (measured at the poles), the ektexine striate, the striae mostly parallel.[2]

DISTRIBUTION. Hill slopes, mixed woods, and thickets in upland areas of Kwangtung and Kwangsi, China. According to a recent publication,

[2] Pollen samples were removed from herbarium specimens, acetolyzed according to the method outlined in Erdtman (1966), and mounted in glycerin jelly. All slides are deposited at the Pollen Laboratory, Department of Botany, Smithsonian Institution. Due to a paucity of material, measurements are based on only 10 grains and should, therefore, be treated with reserve. Material for the scanning electron microscope was acetolyzed and mounted in a mixture of alcohol-water. After evaporation, the grains were vacuum-coated with gold, examined, and photographed with a Cambridge Stereoscan MK II A microscope. The data on pollen morphology were contributed by Joan Nowicke, Palynologist, Smithsonian Institution, Washington, D. C.



FIGURES 3, 4. Scanning electron micrographs of pollen grains of *Sinoradlkofera minor* from (*Wang*) *Sun Yat-sen University 40934*: 3, equatorial view, × 4850; 4, enlargement of ektexine, × 10,000.

Iconographia Cormophytorum Sinicorum (1972), the distribution of the new genus extends to the adjacent provinces of Hunan and Kweichow, where it grows at an altitude of 400 meters. Flowering May and June; fruiting to November.

SPECIMENS EXAMINED. **China.** KWANGSI: Ching-Si Hsien, Piao-Lin village, 24 Aug. 1935, (*Ko*) *Sun Yatsen University 55599* (A); Lung-mu-an and vicinity, Hai-yang-p'ing (Tai-hü P. O.), Kwei-lin District [25.17N, 110.17E], 7 July 1937, *Tsang 27766* (A, NA, US), 8 July 1937, *Tsang 27780* (A, NA, US); Lung-mu-an and vicinity, Hai-yang Shan, Kwei-lin District [25.17N, 110.17E], 8–12 July 1937, *Tsang 27817* (A, NA, UC, US); San-min village and vicinity, P'an-ku-shan and Ch'ao-t'ien-shan, Kwei-lin District [25.17N, 110.17E], 5–23 Aug. 1937, *Tsang 28000* (A, NA, UC, US); Nam Tanyuen (probably Nan Tan Hsien) [24.59N, 107.32E], 28 June 1937, (*Wang*) *Sun Yatsen University 40934* (A); without locality, (*Wang*) *Sun Yatsen University 41208* (A). KWANGTUNG: Yu-yuen Hsien, Tai Chiao [24.46N, 113.16E], 19 Nov. 1934, *Ko 54793* (PE); Lienchow River [ca. 24.30N, 112.30E], Aug. 1887, *Ford 291* (HK, K, NA, photo).

Sinoradlkofera minor is not, as Hemsley thought, a miniature tree only 13 feet tall. Specimens have been collected from plants up to 20 meters in height ((*Wang*) *Sun Yatsen University 40934*). At present, little is known about the ecology and total distribution of the new genus.

ACKNOWLEDGMENTS

My thanks are extended to the herbarium curators for supplying the materials that made this study possible. Dr. Joan Nowicke, palynologist, of the Smithsonian Institution, Washington, D. C., contributed the scanning electron microscope evaluation of the pollen. The Latin diagnosis was prepared by Elaine Mathers.

I am most grateful to my wife, Lillian, for the drawing, which includes the first published details of the flowers of the new genus.

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PTEROCARYA ESQUIROLII, A MISNOMER FOR KOELREUTERIA BIPINNATA

FREDERICK G. MEYER

THE NAME *Pterocarya esquirolii* Léveillé (Juglandaceae), published in Léveillé's *Catalogue des Plantes du Yun-Nan* (1916), p. 135, was based on a single collection, *Esquirol 798* (E), obtained in Kouy-Tcheou (Prov. of Kweichow), China. In the original publication, the specific name was incorrectly spelled "*Pterocarya esquirelii*," which may be assumed to have been a typographical error.

The flowers in the Esquirol material show that the plant clearly belongs to the genus *Koelreuteria* (Sapindaceae), specifically *K. bipinnata* Franchet. The Esquirol specimen and the nomenclatural aspects were inadvertently omitted from my monograph on *Koelreuteria* (Jour. Arnold Arb. **57**: 129–166 (1976).

Thanks are extended to Dr. L. A. Lauener, curator of the Léveillé herbarium at the Edinburgh Botanic Garden, for bringing this matter to my attention.

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A NEW SPECIES OF OREOMYRRHIS (UMBELLIFERAE, APIACEAE) FROM NEW GUINEA

MILDRED E. MATHIAS AND LINCOLN CONSTANCE

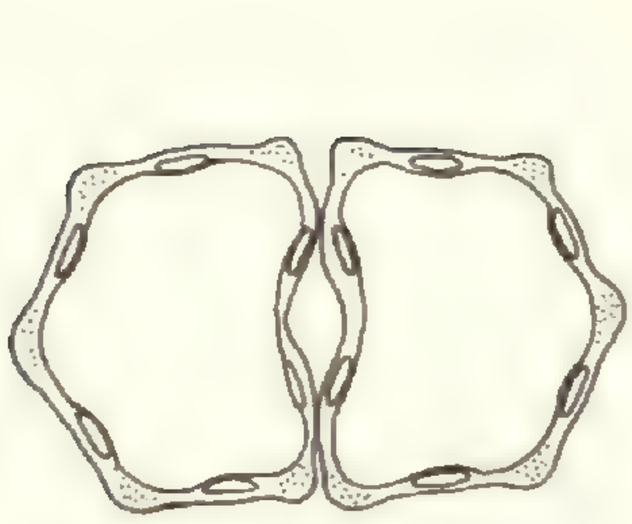
WHEN WE PUBLISHED a world revision of *Oreomyrrhis* some twenty years ago (in Univ. Calif. Publ. Bot. 27: 347–416. 1955), even the two dozen collections then available from New Guinea clearly revealed that the island had a disproportionately large representation of the more striking variation exhibited by this remarkable circum-austral genus. Extensive subsequent collections suggest that our treatment is no longer adequate, but we are not in a favorable position to undertake a re-study. We would, however, like to put on record a striking new taxon that has generously been brought to our attention by the collectors, Dr. P. F. Stevens of the Arnold Arboretum, Harvard University, and Dr. J. F. Veldkamp, Rijksherbarium, Leiden, Netherlands.

Oreomyrrhis plicata M. E. Mathias & L. Constance, sp. nov.
FIGURES 1–6.

Plantae acaulescentes e caudice crasso ligneo, 5–15 cm. altae; folia ambitu linearia vel lanceolata, 1–4 cm. longa, 1–3 mm. lata, plicata, pinnata, foliolis 5–11, linearibus vel lineari-oblongis 2–5 mm. longis integris approximatis obtusatis glabris vel ciliatis carnosis vel coriaceis nitidis ad rhachin articulatam affixis, petiolis gracilibus laminas plerumque aequalibus vel eis longioribus basi late scarioso-vaginantibus, 0.8–6 cm. longis; pedunculi solitarii vel plures apice sparsim retrorso-hirsutuli erectiusculi quam petioli valde longiores, 2.5–12 cm. longi; bracteae involucrales 6–8, lineares vel lanceolati-oblongae obtusae integrae interdum ciliatae dorso glabrae basi connatae quam fructus breviores; flores 10–20 quam involucra breviores, petalis purpureis dorso glabris; stylopodium obscure conicum, stylis divergentibus, stylopodium cum stylis 0.3–0.5 mm. longis; carpophorum usque ad basim bifidum; pedicelli patentes aliquantum crassi adpresso-hirsuti 3–7 mm. longi quam involucrum breviores id aequantes; fructus 10–20 pyriformi-ovoidei valde acuminati glabri, 2.5–3 mm. longi, 1.5 mm. lati, costis prominentibus pallidis quam intervallis fuscis multo angustioribus; vittae in valleculis 1 in commissuris 2; semina facie anguste concava.

TYPE LOCALITY. **Papua New Guinea:** summit of Goë Dendeniwa, Goropu Mountains (Mt. Suckling complex), alt. 3625 m., Raba Raba Subdistrict, Milne Bay District, Lat. 9° 45′ S, Long. 148° 58′ E, 26 June 1972, *Stevens & Veldkamp LAE 54276* (L, holotype; A, isotype).

OTHER COLLECTION. **Papua New Guinea:** Subalpine grasslands, S ridge of Goë Dendeniwa, SW slope in recent rock slide, 3325 m. alt., Lat. ca. 9° 40′ S, Long. 148° 56′ E, 24 June 1972, *Veldkamp & Stevens 5748* (L, UC).



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FIGURES 1–6. *Oreomyrrhis plicata*: all from *Veldkamp & Stevens 5748*. 1, habit, × ½; 2, foliage leaf, × 1; 3, fruiting umbel, × 2½; 4, petal, × 9; 5, intact mature fruit, × 7; 6, fruit transection, × 10.

Mr. Th. van de Water, a student at Leiden, made the initial determination that the new taxon was not included in our monograph. The simply pinnate leaves, folded lengthwise, with closely adpressed linear to linear-oblong leaflets, have not been encountered heretofore in the genus. The type collection is stated to have been made in a "red rock area (ultramafic rock)," and to have been common, but with little associated vegetation except Caryophyllaceae, Ericales, and *Hypericum*.

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COVER: The conelike follicetum or fruit aggregate of *Magnolia tripetala* L., an American species of section Rhytidospermum Spach, is the basis for our new cover design. Individual follicles of the fruiting body were used in the devices for other parts of the Journal and for the offprints. The designs were all drawn by Karen S. Velmure, who also planned and prepared the three preceding covers for the Journal, as well as the accompanying devices.

The section Rhytidospermum, of which *Magnolia tripetala* is the type, includes three species of Asia and four to six of America. These are large shrubs or deciduous trees with leaves crowded into false whorls at the end of branchlets, alternate and widely spaced on new shoots. *Magnolia tripetala*, the umbrella-tree or elkwood, is native in rich woods of eastern North America from southern Pennsylvania and West Virginia, south into Florida, and westward through Ohio and Kentucky to Arkansas and Missouri. It is sometimes found escaped from cultivation north into central Massachusetts. In cultivation it has been involved in many hybrid combinations.

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NORTH AMERICAN COTTONWOODS (POPULUS, SALICACEAE) OF SECTIONS ABASO AND AIGEIROS

JAMES E. ECKENWALDER

AS A RESULT of research on *Populus* L. in southwestern North America (including Mexico), I have made taxonomic decisions that require changes of name for several cottonwoods. The following review, while not monographic in scope, provides sufficient evidence to justify the new status accorded to several well-known taxa, as well as to warrant the description of a new section and a new subspecies in this rather crowded small genus. The morphological, distributional, ecological, and paleobotanical information used here to substantiate these innovations may contribute to further discussion of the systematics of these conspicuous but poorly understood trees.

In addition to major synonyms, I have included major misapplied names. These *sensu* names, which have no direct nomenclatural status, are too often intermingled with the true nomenclatural synonyms. Nonetheless, these misapplications may be of considerable interest for taxonomy, and I have followed Recommendation 50D of the International Code of Botanical Nomenclature for their presentation. I have also included a key to all sections of the genus. This should help to clarify the mutual relations of these taxa and to place the newly described sect. ABASO. The key to cottonwoods of sect. AIGEIROS is the first to include all extant North American taxa.

WORLD KEY TO SECTIONS OF POPULUS

A. Anthers elongate, apiculate at apex; disc of female flower deeply lobed or laciniate.
  B. Plants with markedly heteroblastic leaf development: leaves of juvenile plants linear, those of adults broader; disc of female flower caducous.
    C. Leaves entire or with few large, coarse teeth; carpels (2–)3; ovules >30 per placenta. ..... sect. TURANGA Bunge.
    C. Leaves minutely serrate for most of their length; carpels 2(–3); ovules <15 per placenta. ..... sect. ABASO Eckenwalder.
  B. Plants without markedly heteroblastic leaf development: leaves of both juvenile and adult plants broadly ovate; disc of female flower persistent

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or only tardily deciduous. ..... sect. LEUCOIDES Spach.

A. Anthers short and broad, truncate or emarginate at apex; disc of female flower with entire margin, or slightly sinuately lobed, or minutely dentate.
D. Winter buds only slightly resinous or densely tomentose; floral bracts ciliate; stamens 5–12(–20); disc of female flower narrowly cup-shaped, usually markedly oblique; stigmas 2- or 3-lobed, segments linear; carpels 2. .... sect. POPULUS (= sect. LEUCE Duby) (aspens, white poplars).
D. Winter buds very resinous, if pubescent then not tomentose; floral bracts not ciliate; stamens (8–)20–80; disc of female flower broadly cup-shaped or reduced, only slightly oblique; stigmas 2-lobed, segments broadly expanded, sometimes convoluted; carpels 2–4.
E. Leaves generally not deltoid, markedly heterolateral: upper surface dark bright green, lacking a narrow translucent margin; lower surface white, glaucous, often somewhat discolored by streaks of orange resin; petioles terete, often channeled above. ..... sect. TACAMAHACA Spach (balsam poplars).
E. Leaves ± deltoid, not heterolateral: both upper and lower surfaces light green, with a narrow translucent margin, not markedly glaucous beneath, sometimes marked by streaks of milky resin; petioles laterally compressed near junction with leaf blade (or, if resembling sect. TACAMAHACA in some of these characteristics, the leaves markedly deltoid to trullate). ..... sect. AIGEIROS Duby (cottonwoods, black poplars).

Populus sect. **Abaso** Eckenwalder, sect. nov.

Gemmae hyemales leviter viscosae, crassae, stramineae; bracteolae lineares, laciniatae ad apices; perigonia florum marum vadose cyathiformia, obliqua, lobata; stamina apiculata; perigonia florum femineorum praealte cyathiformia caduca e zona abscissionali bene evoluta, tenuissima, e base ad latum divisa, laciniata; capsulae bivalvae (raro trivalvae); stylum unicus; stigmata aliquantum tumida, cucullata, convoluta.

SPECIES TYPICA: *Populus mexicana* Wesmael.

Abaso is the Cáhita folk name for *P. mexicana*. This species is most abundant in the Cáhita territory of Sonora and Sinaloa. No other extant species of the section is known at present.

All authors from Wesmael (1868) to Wiggins (1964) who have treated *Populus mexicana* have evidently considered it a member of sect. AIGEIROS. Most of these authors had only sterile material or mature capsules available. Leaves of adult trees of *P. mexicana* are broadly deltoid and long-acuminate. They somewhat resemble those of sect. AIGEIROS, cottonwoods, especially those of *P. nigra* L. of Eurasia and North Africa. The capsules are also superficially reminiscent of those of members of sect. AIGEIROS, so assignment to this section was quite reasonable. However, examination of flowering material from my own and other collections shows that the floral and vegetative characteristics of *P. mexicana* contrast strongly with those of sect. AIGEIROS. The apiculate anthers and laciniate, caducous disc of the female flowers in *P. mexicana* contrast with the

emarginate anthers and entire, sometimes reduced, persistent disc usual in sect. AIGEIROS. The juvenile leaves, which are linear in *P. mexicana* and rhomboid in members of sect. AIGEIROS, can also be used to distinguish the two taxa. Furthermore, winter buds of *P. mexicana* are stout, blunt, dry, and bright yellow and differ from the elongated, sharp-pointed, resinous, tan to red buds of the AIGEIROS cottonwoods. Lastly, *P. mexicana* has more numerous catkins per shoot (often 10–15) than do the AIGEIROS cottonwoods (usually 2–5), and it sometimes has a leaf on the proximal portion of the catkin, a primitive condition never found in representatives of sect. AIGEIROS.

These characteristics of *Populus mexicana* resemble those of species of sect. TURANGA (including sect. TSAVO (Jarmolenko) Browicz) of the old-world tethyan arid zone from Spain and Morocco to Mongolia. The new-world plants, however, differ from those of the Old World in their different leaves as well as in their much lower seed number and fewer carpels. Furthermore, the old-world *P. euphratica* Oliver and its allies invariably display sympodial growth with abortion of the shoot apex (Kimura, 1938; Browicz, 1966), while this habit is only incompletely established in sect. ABASO. Sections ABASO and TURANGA are more strongly separated than the universally accepted sects. AIGEIROS and TACAMAHACA, which differ only in vegetative characters. Differences between sects. ABASO and LEUCOIDES are even greater, and there is little beyond generic resemblance between sect. ABASO and sects. POPULUS and TACAMAHACA.

Poplars resembling sect. ABASO are first known from the Eocene Green River Formation of Colorado, Utah, and Wyoming. *Populus cinnamomoides* (Lesquereux) MacGinitie (= *P. wilmattae* Cockerell), known only from leaf remains, has the narrow juvenile leaves and broad, long-acuminate adult leaves of sect. ABASO, as well as similar details of venation (MacGinitie, 1969; Eckenwalder, unpubl.). Similar leaves have been found in nearly contemporaneous deposits of the Puget Group in Washington (J. A. Wolfe, pers. comm.) and in the Claiborne Flora of Texas and Tennessee (Berry, 1916, 1930; as *Banara eocenica* Berry (Flacourtiaceae) and *Grewiopsis tennesseensis* Berry (Tiliaceae)). Beyond continued presence in Oligocene deposits of the Ruby Basin of Montana (Becker, 1972; Eckenwalder, unpubl.), this section has no further known fossil record, leaving a gap of more than 25 million years between the last known fossil occurrence and the present.

Populus mexicana Wesmael in DeCandolle, Prodromus 16(2): 328. 1868. TYPE: Mexico, entre Tampico [Tamaulipas] et Real del Monte [Hidalgo], May 1827, *Berlandier 274* (holotype, G–DC (IDC B-800. 2766: I. 1.!); isotypes, G, MO!).

This species, with its strongly heteroblastic leaf development marked by distinctive willow-like leaves of the juvenile phase, consists of two subspecies, one from each coast of Mexico. I include an illustration of this species (FIGURE 1), which has not heretofore been figured.

FIGURE 1. *P. mexicana* subsp. *dimorpha*: A, flowering shoot; B, ♂ catkin; C, ♂ flower with bract; D, stamen; E, ♀ catkin; F, ♀ flower with bract; G, fruiting catkin; H, inside of capsule valve showing seed attachments; I, shoot of juvenile plant; J, mature adult leaf. *P. mexicana* subsp. *mexicana*: K, mature adult leaf. (A–D from *J. E. Eckenwalder 17*; E, F from *J. E. Eckenwalder 22*; G, H, J from *J. E. Eckenwalder 397*; I from *J. E. Eckenwalder 20*; K from *J. E. Eckenwalder 448*. All specimens at UC.)

Populus mexicana subsp. **mexicana.**

Populus arizonica auct. non Sargent; Miranda, La vegetación de Chiapas **1:** 143, 145, 146, 184, 185. 1952.

This cottonwood has been poorly understood ever since its description in 1868. Wesmael (1869) himself expressed doubts as to its distinctness from *P. nigra* of Europe and subsequently (1887) placed it in the synonymy of the later described *P. fremontii* S. Watson. The name *P. mexicana* was often misapplied to *P. fremontii* subsp. *mesetae* Eckenwalder, the AIGEIROS cottonwood of the central plateau of Mexico, in herbarium identifications (Sargent, 1902 and 1919a). The type material (*Berlandier 274*), although sterile, clearly belongs to the uncommon but widespread ABASO cottonwoods of rivers of the Gulf of Mexico Coastal Plain from near Monterrey to the state of Veracruz. *Populus mexicana* subsp. *mexicana* also occurs in mountains of Oaxaca and Chiapas (the southernmost station for *Populus* in the New World). This cottonwood has often been misidentified in herbaria as *P. arizonica* Sargent (= *P. fremontii* subsp. *fremontii*) of sect. AIGEIROS, from which it differs in the lack of pubescence on shoots, buds, and leaves, in addition to characteristics given in the sectional key.

Populus mexicana subsp. **dimorpha** (T. S. Brandegee) Eckenwalder, comb. et stat. nov.

Populus dimorpha T. S. Brandegee, Zoë **5:** 197, 198. 1905. TYPE: Mexico, Sinaloa: Culiacán, 20 Aug. 1905, *T. S. Brandegee s.n.* (holotype, UC!; isotypes (dated *22* Aug.), F!, GH!, NY!, POM!).

Because of the obscurity surrounding the identity of *Populus mexicana* subsp. *mexicana* (Standley, 1920), and also because the willow-like juvenile leaf phase which Brandegee noted for his plants (and used as the basis for his epithet) has hitherto been unknown in the typical subspecies, no previous author has admitted a relationship between the uncommon trees of eastern Mexico and the abundant cottonwood of Coastal Plain rivers of the west. One Veracruz specimen, however, was identified as *P. dimorpha* by the Flora of Veracruz project. Nonetheless, the two populations agree in most features of floral structure, as well as in shoot and bud characters and in their pattern of heteroblastic leaf development. They differ in the predominant leaf shape of adult trees, with leaves of subsp. *dimorpha* longer acuminate than those of subsp. *mexicana* (FIGURE 1J, K). They also differ in number of ovules per placenta of otherwise similar capsules (6–9 in subsp. *mexicana*, (8–)11–15 in subsp. *dimorpha*). The southern inland populations of Oaxaca and Chiapas are somewhat intermediate in these characteristics, further strengthening the link between the two taxa. *Populus mexicana* subsp. *dimorpha* occurs on floodplains of all major perennial rivers of the western Coastal Plain from the Rio Yaqui (Edo. Sonora) to the Rio Piaxtla (Edo. Sinaloa). It is abundant in the northern valleys, although quite rare from the Rio San Lorenzo (Edo. Sinaloa) southward.

Populus sect. **Aigeiros** Duby, Botanicon Gallicum 1: 428. 1828. TYPE: *Populus nigra* Linnaeus, Sp. Pl. 2: 1034. 1753.

These are the lowland riparian cottonwoods of the great rivers from coast to coast across the central portion of North America. Different authors have recognized from one to ten species of this section in southwestern North America (Sargent, 1922). With removal of *P. mexicana* into sect. ABASO, the remaining taxa form a rather homogeneous group, which has been designated subsect. AMERICANAE Bugała (1967) in contradistinction to the old-world subsect. EUROASIATACAE Bugała. These cottonwoods are characterized by large, tan, setose, resinous winter buds, many stamens, 3–4-carpellate, glabrous ovaries, and large, platelike stigmas. The distinctive early leaves (those of the spring flush) of all are broadly deltoid-ovate, coarsely crenate-dentate in the middle portion, and with an abrupt, long, toothless, acuminate apex. Within this framework of similarity, however, there are substantial differences between local populations (Marcet, 1962). Among characters that show considerable variation are various aspects of leaf shape (FIGURE 2), basilaminar glands, pubescence, pedicel length, stamen number, disc shape and width, capsule shape, and ovule number. The distribution of variation can be divided geographically in many ways, which accounts in part for the diversity of species treatments in this group. Geographic variation patterns of several characters are only partially correlated, but disc width and some other floral characteristics seem to follow broad geographic outlines. Each population occupying a distinct drainage system has a distinctive facies, although, insofar as is known, all populations are fully interfertile (Stout & Schreiner, 1933; Zsuffa, 1975; Eckenwalder, unpubl.). These populations cohere into five major geographic races worthy of formal taxonomic recognition, and the races can be further grouped into eastern and western taxa. On this basis, I recognize only two extant species of North American AIGEIROS cottonwoods, each with subspecies. The geographic boundaries between these species and subspecies are zones of character state shift for the greatest number of characters.

Fossilized leaves from western North America attributable to sect. AIGEIROS are widespread in Pliocene deposits where they have been assigned names such as *Populus prefremontii* Dorf and *P. lamottei* Chaney & Elias (LaMotte, 1952). The only earlier remains known are specimens of *P. russellii* Knowlton from late Miocene horizons of the Ellensburg Flora of central Washington (Smiley, 1963). None of these forms, in the absence of reproductive material, shows particularly close relationships to either of the extant species, although they are quite similar to both. Pleistocene remains, equally undiagnostic, have been assigned to extant taxa (LaMotte, 1952; Axelrod, 1966).

KEY TO NATIVE NORTH AMERICAN TAXA OF SECT. AIGEIROS

A. Floral disc broad in fruit, 5–9 mm. wide, deeply cup-shaped; pedicels short, 4 mm. long; young shoots and petioles often pubescent. . . *Populus fremontii*.

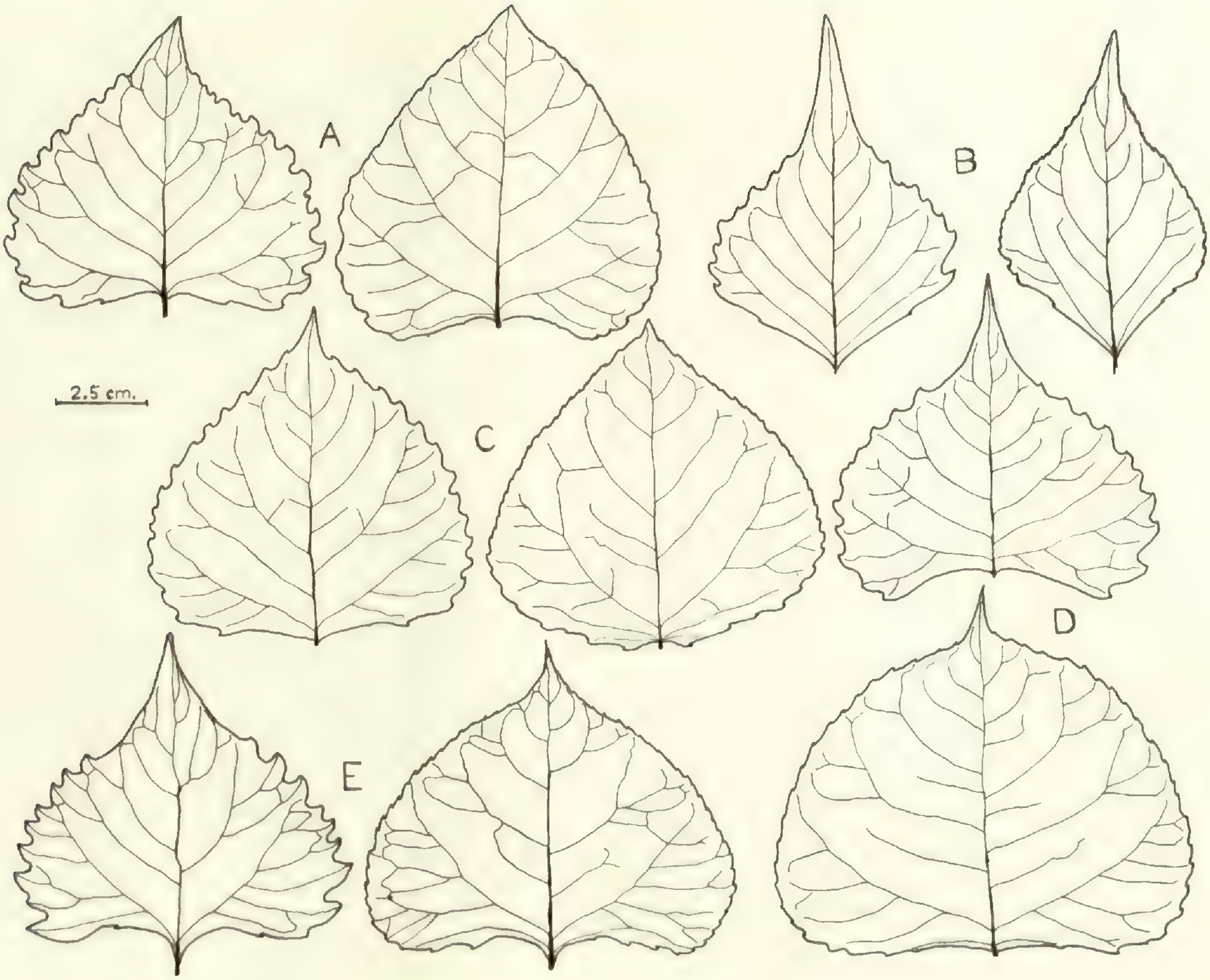

FIGURE 2. Representative early leaves (left or above) and late leaves (right or below) of native North American sect. AIGEIROS cottonwoods: A, *P. fremontii* subsp. *fremontii*, *J. E. Eckenwalder 904* (UC); B, *P. fremontii* subsp. *mesetae*, *J. E. Eckenwalder 408* (UC); C, *P. deltoides* subsp. *deltoides*, *J. L. Strother 1226* (UC); D, *P. deltoides* subsp. *monilifera*, *D. S. Correll & I. M. Johnston 17103* (TEX); E, *P. deltoides* subsp. *wislizenii*, *J. E. Eckenwalder 237* (UC).

B. Shoots with orange cast, usually densely pubescent; late leaves (those initiated and expanding during current growing season) and early leaves of slender and lateral shoots often trullate, cuneate at base, longer than wide, long-acuminate. ..... *P. fremontii* subsp. *mesetae*.

B. Shoots with yellow or gray cast, glabrous to densely pubescent; late leaves broadly deltoid, usually truncate or cordate at base, occasionally broadly cuneate, often as wide as or wider than long, short-acuminate or acute. ..... *P. fremontii* subsp. *fremontii*.

A. Floral disc reduced in fruit, 1–4 mm. wide, flat to shallowly cup-shaped; pedicels short to long, ≤15 mm. long; shoots and petioles glabrous. .... *Populus deltoides*.

C. Pedicels uniformly short, <6 mm. long; leaves often long-acuminate, usually with 2 basilaminar glands (or none). .... *P. deltoides* subsp. *monilifera*.

C. Pedicels longer, up to 15 mm. long; leaves usually short-acuminate, with 0–5 basilaminar glands.

D. Pedicels nearly uniformly long along the catkin; leaves without basilaminar glands; late leaves broadly deltoid, usually as wide as or wider than long; winter buds pubescent; emergent leaves glabrous. ..... *P. deltoides* subsp. *wislizenii*.

D. Pedicels long proximally, much shorter distally along the catkin; leaves usually with 3–5 basilaminar glands; late leaves broadly ovate, usually distinctly longer than wide; winter buds glabrous; emergent leaves pilose. ..... *P. deltoides* subsp. *deltoides*.

Populus fremontii S. Watson, Proc. Am. Acad. Arts **10**: 350. 1875. SYNTYPES: California, Tehama Co., Deer Creek at Lassen's, 1846, *Fremont 243* (♀) and *244* (♂) (lectotype (here designated), *243* (♀) at GH; isolectotype, NY!).

This species is treated by various authors either as the sole southwestern AIGEIROS cottonwood (Little, 1953) or as a Californian representative of a series of local species (Sudworth, 1934). The broader view adopted here emphasizes the similarities of diverse populations of this species in possessing short pedicels and in the broad, cup-shaped floral disc enclosing the lower portion of the fruit. In addition, most individuals have globose capsules and more or less yellowish-green leaves that are tomentose with short, yellow-tinged hairs, as are the first-year shoots, although glabrous individuals are fairly common, especially in northern California. Furthermore, there is a tendency for leaves of *Populus fremontii* to be smaller and thicker than those of *P. deltoides*, as well as to have fewer teeth and a shorter apex (FIGURE 2), but there is much overlap in these characteristics. Variation within *P. fremontii* seems best treated by segregating populations from east and west of the continental divide as two subspecies, a disposition which has in essence been followed by authors who have treated these population systems as two species, *P. fremontii* and *P. arizonica* Sargent (Johnston, 1944).

Populus fremontii subsp. **fremontii**

Populus macdougalii Rose, Smithson. Misc. Collect. **61**(12): 1, 2. 1913.
Populus arizonica Sargent, Bot. Gaz. (Crawfordsville) **67**: 210. 1919.
Populus arizonica var. *jonesii* Sargent, *op. cit.* 211.
Populus fremontii var. *pubescens* Sargent, *op. cit.* 213.

These plants vary from quite glabrous for many trees of northern cismontane California, to densely pubescent in the Mojave Desert and other regions. In general, this subspecies is much more variable than is the following, with several distinctive local variants. For instance, many trees of the lower Colorado River and the Salton Basin have the floral disc of the fruit much reduced, and in this respect resemble *Populus deltoides*. These trees have been segregated as *P. macdougalii*, but a broad spectrum of intermediates between them and "typical" *P. fremontii* occurs in this same region. Similarly, juvenile individuals with rhomboid rather than deltoid leaves occur scattered throughout the range, and are referred to *P. arizonica* in California (Munz, 1959). Much of this and other variation in leaf form can be attributed to the diameter of the shoot (and ultimately of the shoot apex) that bore them, as pointed out by Dode (1905). In general, trees of subsp. *fremontii* have larger, very broad, deltoid early and late leaves with truncate or cordate bases, and may thus be distinguished from subsp. *mesetae* (FIGURE 2A, B). In this broad view, *P. fremontii* subsp. *fremontii* occurs west of the continental divide from the rim of the Sacramento Valley (California) and the western flanks of the Wasatch Range (Utah), south through Arizona to northern Baja California and Sonora, with outliers in Nevada and southwestern New Mexico.

Populus fremontii subsp. **mesetae** Eckenwalder, subsp. nov.

Populus mexicana auct. non Wesmael; Sargent, Silva of North America **14**: 73, 74. *pl. 733*. 1902.
Populus arizonica auct. non Sargent; Johnston, Jour. Arnold Arb. **25**: 434, 435. 1944. Correll, Flora of Texas **3**: 397–399. *pl. 58*. 1961.

A *P. fremontii* typica differt statura aliquantum inferiore; pubescentia ramuli novelli ochracea, confertiore; foliis aestivalibus trullatis non deltoideo-ovatis, base cuneatis vel rotundatis, rariore truncatis, non subcordatis; bracteolis angustioribus.

TYPUS: Mexico. Chihuahua: Valley near Chihuahua, 31 Mar. 1886, *Pringle 885* (holotype, UC!; isotypes, F!, GH!, MO!).

Populus fremontii subsp. *mesetae* derives its name from the Meseta Central of Mexico where it is primarily distributed.

Tree 6–20 m. tall, 2–12 dm. d.b.h.; trunk dividing near base into 2 or 3 major branches, ascending at a low angle and spreading to form a broad oval crown; bark tan and deeply furrowed at base, bone white to light tan and smooth on branches. First year twigs tan, usually densely pubescent with short, soft, ochraceous hairs. Winter buds ovate, yellow-brown,

resinous, sparsely to densely pubescent with short, stiff hairs; terminal vegetative buds and female flowering buds 7–12 mm. long; male flowering buds 11–20 mm. long. Leaf blade yellow green, (2–)4–14 cm. long; early leaves of main shoots broadly deltoid-ovate, about as wide as long, with truncate or subcordate base and short-acuminate, entire apex; late and early leaves of weak shoots trullate, about ¾ as wide as long, with cuneate (rarely truncate) base and long-acuminate, entire apex (FIGURE 2B). Early leaves coarsely serrate with 3–15 crenate teeth on each side of blade; late leaves finely serrate with 10–25 small teeth on each side; petiole 1–9 cm. long, transversely flattened at junction with leaf blade, pubescent. Aments 4–13 cm. long, lax, with 10–30 flowers. Stamens 30–70. Capsule 6–10 mm. long, broadly ovoid to globular, obtuse, 3–4-valved, with 11–18 ovules per placenta; disc 5–8 mm. broad, cup-shaped, enclosing lower portion of fruit; fruiting pedicel 1–3 mm. long. Flowering February to April, fruit maturing April to July.

This cottonwood is common along major rivers of the basins and in canyons of the foothills throughout much of the Chihuahuan Desert region. It extends, mostly east of the continental divide, from southern New Mexico and trans-Pecos Texas south on the Central Plateau to the Valley of Mexico, with a possible outlier in the Chiricahua Mountains, Arizona. Much of its southern distribution appears to be anthropogenic, and it is widely planted about ranches and in towns throughout the region. Isolated individuals are commonly found near springs and other small, perennial sources of water.

Unfortunately, none of the five epithets applied to this well-known tree in the literature and in herbaria can be used under the taxonomic concepts accepted here. Most herbarium specimens are identified as *Populus mexicana* or *P. arizonica*; others as *P. fremontii*, *P. wislizenii* (S. Watson) Sargent, or *P. arizonica* var. *jonesii* Sargent. Johnston (1944) discussed the nomenclature of this cottonwood, which he considered a species distinct from *P. fremontii*. He decided in favor of the name *P. arizonica* Sargent, which he lectotypified by *Pringle 885*, a Chihuahuan specimen. This specimen probably served as the basis for part of *plate 773* of "P. mexicana" in Sargent (1902). Sargent (1919a), after examining a photograph of the type of *P. mexicana* Wesmael, had proposed the name of *P. arizonica* for the cottonwood described as "P. mexicana" in 1902. Thus Johnston argued that *P. arizonica* should be typified by the "major element" in the plate of "P. mexicana" in Sargent (1902). This lectotypification is untenable, however, because Sargent (1919a) specifically excluded *Pringle 885* from *P. arizonica* var. *arizonica*, and assigned it instead to *P. arizonica* var. *jonesii*, described concurrently. The Arizona syntypes of *P. arizonica* are all referable to typical *P. fremontii*. While Sargent assigned all specimens of *P. fremontii* subsp. *mesetae* to *P. arizonica* var. *jonesii*, the type of this variety, *M. E. Jones 3731*, from Baja California, is another specimen of typical *P. fremontii*. Other epithets in the complex are based on specimens from California, Arizona, or New Mexico and

are all referable to *P. fremontii* subsp. *fremontii* as circumscribed here. Thus it is necessary to name here the prominent cottonwood of the arid Mexican plateau, a tree which is one of the largest in the region, is widely planted in the alamedas of Mexican towns, and has been well known to plant explorers for at least a century.

Populus deltoides Bartram ex Marshall, Arbustrum Americanum 103. 1785. TYPE: Carolina and Florida, *W. Bartram* (holotype, BM? (not located)).

Populus canadensis auct. non Moench; Kuntze, Rev. Gen. Pl. 643. 1891.
Populus balsamifera auct. non Linnaeus; Farwell, Rhodora **21:** 101. 1919. Sargent, Jour. Arnold Arb. **1:** 62, 63. 1919.

The taxonomy and nomenclature of this species are rather confused as a result of its early introduction into Europe and of its spontaneous and artificial hybridization there with *Populus nigra* L. Different introductions and hybrids of various provenances each received separate names in the late eighteenth and early nineteenth centuries. In general, however, most European and many American authors have recognized a southern and a northern cottonwood in the eastern United States (Schneider, 1906; Sargent, 1922), although they have not all agreed on the proper names for the two taxa. *Populus canadensis* Moench has occasionally been used for the eastern cottonwood when *P. deltoides* was considered an ambiguous name, but it seems more properly referable to the Euro-American hybrids between *P. deltoides* and *P. nigra* (Boom, 1957). The most awkward nomenclatural upset arose when Sargent (1919b) and Rehder (1927, 1929) adopted Farwell's (1919) suggestion that *P. balsamifera* applied to the eastern AIGEIROS cottonwood, rather than to the eastern TACAMAHACA balsam poplar. This assertion was finally laid to rest by Rouleau (1946), and *P. deltoides* has since remained unchallenged as the name of the eastern cottonwood (Little, 1953).

As defined here, *Populus deltoides* consists of three intergrading subspecies that are distinguished by pedicel, pubescence, and leaf characters outlined in the key. As with *P. fremontii*, each subspecies is quite variable, although the subspecies resemble each other in the long-ovate to elliptic capsules that are subtended by very reduced floral discs and are often borne on highly elongated pedicels, in the darker green leaves that are often larger than those of *P. fremontii*, and in the glabrous shoots. Some aspects of leaf morphology, such as shape, number of teeth, and number of basilaminar glands, show clinal, or even seemingly random, variation (Marcet, 1962; Eckenwalder, unpubl.). Within this context, boundaries of the subspecies enclose the most homogeneous populations with the greatest association of characters.

Populus deltoides subsp. **deltoides**

Populus virginiana Fougeroux, Mém. Agric. Soc. Roy. Agric. Paris 1786. 87–90. 1787.

Populus angulata W. Aiton, Hortus Kewensis 3: 407. 1789.
Populus angulata var. *missouriensis* A. Henry in Elwes & Henry, Trees of Great Britain and Ireland 7: 1811. 1908.

This is the "southern" cottonwood, which extends from the Gulf Coast states northward along the Atlantic seaboard to Massachusetts and northward in the Mississippi embayment region to central Illinois and Ohio. It occurs westward as far as eastern Texas and Oklahoma. Marcet (1962) postulated relatively recent occupation of the northern portion of this range at the expense of the more northerly subsp. *monilifera*, but this, while possible, is not clear from the evidence. *Populus deltoides* subsp. *deltoides* is characterized by its glabrous winter buds and densely pilose emerging leaves and differs from the other two subspecies in its relatively long, broadly ovate, late leaves (FIGURE 2C) with 3–5 tubular basilaminar glands. Early leaves are often quite similar in shape and marginal teeth to those of subsp. *wislizenii*, and the pedicels reach the length of those of subsp. *wislizenii*, but they are more variable in length on the same catkin. Apical pedicels are as short as those of subsp. *monilifera*, but they become longer basipetally (subsp. *monilifera* has uniformly short pedicels within a catkin). The early leaves tend to have shorter points and may have fewer teeth than those of subsp. *monilifera*.

Populus deltoides subsp. **monilifera** (W. Aiton) Eckenwalder, stat. nov.

Populus monilifera W. Aiton, Hortus Kewensis 3: 406. 1789. TYPE: (Canada) cult. Kew Gardens, *W. Aiton* (holotype, BM!).
Populus deltoides var. *occidentalis* Rydberg, Mem. New York Bot. Gard. 1: 115. 1900.
Populus sargentii Dode, Bull. Soc. Hist. Nat. Autun 18: 198. 1905.
Populus deltoides var. *monilifera* (W. Aiton) A. Henry, Gard. Chron. Ser. 3. 56: 2. *fig. 4.* 1914.
Populus texana Sargent, Bot. Gaz. (Crawfordsville) 67: 211, 212. 1919.

Most modern discussion of *P. deltoides* has revolved around the distinctness of the cottonwoods of the Great Plains region from their eastern counterparts (Fowells, 1965). The contrasts of foliar and bud characteristics usually advanced to distinguish a western species (*P. sargentii*) or variety (*Populus deltoides* var. *occidentalis*) from the eastern cottonwood (Sargent, 1913) really apply solely to the southern cottonwood, *P. deltoides* subsp. *deltoides*. The cottonwoods of the Great Lakes and other representatives of the northern cottonwood are, in fact, quite similar to the trees of the plains, and I treat them all as members of a single subspecies. They are similar in their short pedicels, pubescent winter buds. and long-acuminate, deltoid-ovate leaves (FIGURE 2D), generally with a single pair of basilaminar glands (although these are absent in a few Texas plants). There is a general decline in tooth number southwestward from the northeastern part of its range. This subspecies occurs from the

Great Lakes region westward to the Prairie Provinces and south to the Texas panhandle.

Populus deltoides subsp. **wislizenii** (S. Watson) Eckenwalder, comb. et stat. nov.

Populus fremontii var. *wislizenii* S. Watson, Am. Jour. Sci. **15:** 137. 1878. TYPE: New Mexico, on the Rio Grande near Charvis and lower down, below Santa Fe, 20 July 1846, *A. Wislizenus s.n.* (holotype, GH; isotype, MO!).

Populus wislizenii (S. Watson) Sargent, Silva of North America **14:** 71, 72. *pl. 732.* 1902.

Whether they treat the cottonwoods of the upper Rio Grande valley as a separate species (Standley, 1920) or as a variety of *P. fremontii* (Little, 1953), most authors have indicated that these trees have their greatest affinity with the western *P. fremontii.* Little (1971) went so far as to include the distribution of this subspecies as part of that of *P. fremontii* without differentiation in his distribution maps. Only Correll (1961) has pointed out the similarities of these trees to the cottonwoods of the Great Plains, which he treated as the segregate *P. sargentii.* Shoot, bud, and capsule characters all align this subspecies with the eastern *P. deltoides* rather than with *P. fremontii.* Like those of *P. fremontii*, leaves of *P. deltoides* subsp. *wislizenii* lack basilaminar glands but are generally broader (especially the juvenile leaves) with fewer, coarser teeth (FIGURE 2E), features that also distinguish them from leaves of other subspecies of *P. deltoides*. These trees are further distinguished by the uniformly elongated fruiting pedicels.

Populus deltoides subsp. *wislizenii* occupies the upper Rio Grande drainage from near El Paso northward and extends to the Colorado River drainage in northeastern Arizona, eastern Utah, and western Colorado. While the southwestern boundary between this subspecies and *P. fremontii* is quite sharp, there is a narrow zone of intergradation between these taxa in eastern Utah, and there is a broader zone of intergradation of subsp. *wislizenii* and subsp. *monilifera* in southeastern Colorado and adjacent New Mexico and Oklahoma. These zones presumably represent areas of hybridization between mutually fully compatible taxa (Zsuffa, 1975; Eckenwalder, unpubl.), and I postulate further local hybridization between *P. deltoides* subsp. *wislizenii* and *P. fremontii* subsp. *mesetae* in the vicinity of the Davis Mountains in trans-Pecos Texas to account for variation patterns in this area.

The generalized distributions of these species and subspecies outlined above are far from definitive. The distributions (partly derived from those of Sudworth, 1934, and Little, 1972) and the original taxonomic framework presented here are largely based on the abundant, but too often poor, material available in herbaria. Characteristics of few populations are well documented in the collections of any herbarium, and I urge anyone wishing to contribute specimens of this group (and of *Populus*

generally) to gather as full material as possible, ideal documentation requiring three separate collection times. Male and female flowering material appears in early spring (February–April), fruiting material in late spring (May–June). Winter buds mature in late summer (August–October) before the fully mature leaves drop in autumn. Characters useful in the taxonomy of cottonwoods are drawn from this complete phenological cycle. It is important in gathering leaf material to gather whole long shoots (from last year's bud scale scars to the shoot apex), since early leaves (those of the spring flush) often differ in form from late leaves (those produced during the current growing season; Critchfield, 1960), and both types show useful taxonomic characters. Midsummer collections with neither fruits nor winter buds and winter collections showing only shoot characteristics are, unfortunately, rather more common in herbaria than the more useful kinds of specimens described above. Further progress in cottonwood systematics will depend, in large part, on better documentation of many populations along the lines suggested here.

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LEAF VENATION PATTERNS OF THE GENUS HIBBERTIA (DILLENIACEAE)[1]

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LEAF VENATION STUDIES have recently provided valuable taxonomic data about both fossil and living plants (Dilcher, 1974; Dolph, 1974; Hickey, 1973; Hickey & Wolfe, 1975; Mouton, 1970), although the venation patterns of leaves have long been neglected in taxonomic and descriptive studies (Foster, 1959). Hickey (1973) recognized the general neglect of various leaf characters in angiosperm systematics and noted the occurrence of incorrect generic assignments of fossil leaves which resulted from the consideration of superficial morphological characters only. He attributed this to the lack of a standardized system of leaf-character classification and responded by modifying and expanding the terminology of von Ettingshausen (1861) to devise a system of so-called leaf architectural classification (Hickey, 1973). Hickey (*loc. cit.*) felt that this classification system might serve as a valuable taxonomic tool, in view of the general consistency of the venation patterns in most dicotyledons. Both Hickey (1973) and Wolfe (1973) anticipated the value of such a classification in ecological and phylogenetic studies of woody dicotyledons, and Dilcher (1974) has stressed the importance of Hickey's classification scheme in evolutionary studies.

Early investigations concerning leaf venation were generally restricted to a single genus or species and often described the mature venation pattern with respect to its ontogeny (Foster, 1950a, b, 1951; Pray, 1954, 1955a, b, c, 1959; Ramji, 1961). More recently, comparative surveys of mature venation patterns in families and genera of dicotyledons have been presented (e.g., Dede, 1962; Vargheese, 1966; Sehgal & Paliwal, 1974). Hickey and Wolfe (1975), in a comprehensive synthesis of dicotyledonous leaf venation patterns, have utilized leaf architectural features to construct a synoptic key to dicotyledonous leaves following the subclasses of Cronquist (1968). However, the relative paucity of such studies emphasizes the need for further intensive surveys of leaf venation patterns in the systematic treatments of modern taxa.

The Dilleniaceae, a woody dicotyledonous family little studied since the taxonomic work of Gilg and Werdermann (1925), has been the subject of recent comparative morphological studies (Wilson, 1965, 1973; Dickison, 1967a, b, 1968, 1969, 1970a, b). This family is of particular interest since it is thought to occupy a key position with respect to angiosperm phylogeny (Dickison, 1967a). Stebbins (1974), for example, stated that the

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Dilleniaceae is the most primitive extant family of angiosperms that exhibits a wide range of ecological preferences.

Hibbertia Andrews is the largest genus of Dilleniaceae and contains an estimated 150 species. These plants are mostly small, erect, much-branched shrubs under two meters tall, although some New Caledonian species reach a height of ten meters. Very few species are scandent, *H. dentata* and *H. scandens* being the only species which are clearly vines. Leaves are simple, of various shapes, and range from large to extremely small and scalelike. They are spirally arranged in all species except *H. coriacea* Baillon, which is endemic to Madagascar and has an opposite leaf arrangement. The leaves commonly have reflexed margins along with other xeromorphic specializations such as reduced size and stomatal crypts or grooves (Dickison, 1970a). Dense mats of trichomes are also commonly associated with the xeromorphic leaf forms.

Interpretations of inflorescence morphology among *Hibbertia* species vary. Hoogland (1951) reported that the inflorescences are dichasial and usually reduced to a few-flowered pseudo-raceme, spike, or solitary flower. Stebbins (1974, p. 264), however, stated that dichasia are not found in *Hibbertia*. The flower or inflorescence may be terminal or axillary, and the flowers are sessile or short-pedicellate. Flowers are conspicuous and usually have a yellow corolla composed of three to five members, although color may range from orange to white. Bracts and bracteoles are often present and may be poorly differentiated from the five, often bractlike sepals. Stamen number ranges from one to over 200, and the stamens may or may not be located along one side of the gynoecium. Staminodia are present in some species, and the stamens are either free or basally connate to form fascicles. Anthers dehisce longitudinally and introrsely or poricidally. The number of carpels ranges from one to five but may, occasionally, be greater (8–15 in *H. grossulariifolia*). They are free or basally connate and contain from 1–15 ovules borne upon a submarginal placenta. Styles are filiform and curved or recurved. The fruit is a follicle which dehisces along its inner suture to release 1–15 arillate seeds. On the basis of floral structure, *Hibbertia* is the most primitive genus in the family (Dickison, 1968).

The distribution of *Hibbertia* is latitudinally restricted between the equator and ca. 40° south latitude (van Balgooy, 1966). The genus is located primarily in Australia (including Tasmania), where approximately 125 species occur. Approximately 24 species are distributed in New Caledonia, and a single species occurs in both Madagascar (*H. coriacea*) and Fiji (*H. lucens*).

Hibbertia is found in lowland dunes, hills, and mountains up to 3000 meters in New Guinea. It also occurs in open forests, savannahs, or heaths, along rivers, and occasionally in bogs or in rain forests. It grows mostly on dry, sandy, or gravelly soil but is also known to inhabit loamy or clayey soils (van Balgooy, 1966).

The extraordinary diversity of *Hibbertia*, with respect to growth habit and floral structure, has been emphasized by Stebbins (1974). Dickison

(1970a) also commented upon the great anatomical diversity of the leaves, as well as on anatomical adaptations to extreme environmental conditions. Stebbins (1972, 1974) has illustrated how this genus provides, as does the entire family, a model to illustrate presumed adaptive radiation from intermediate habitats toward both more mesic and more xeric adaptations.

Recent workers (Hickey, 1971a, b; Hickey & Wolfe, 1975; Wolfe, 1973) have outlined relative levels of evolutionary specialization for leaf venation patterns in woody dicotyledons. If one assumes that venation patterns are indicative of various levels of phylogenetic advancement, an attempt to correlate these patterns with previously "established" phylogenetic trends in *Hibbertia* would be most informative. Positive correlations would serve to strengthen hypotheses regarding the organization of primitive and advanced leaf venation patterns in woody dicotyledons. Therefore, the objectives of this investigation are: (1) to describe the entire range of major and minor leaf venation patterns in *Hibbertia* Andr.; (2) to determine the consistency of venation patterns observed within the established sections and subsections of the genus; (3) to seek correlations between foliar venation patterns and evolutionary trends observed elsewhere in the plant body; and (4) to interpret such correlations, where possible, from an ecological and evolutionary perspective.

MATERIALS AND METHODS

Leaves of 97 species of *Hibbertia* Andr., representing all but one (Sect. V. Oligostemon) of the subgeneric sections of Gilg and Werdermann (1925), were studied. Leaves were cleared in 5 percent NaOH (Bailey & Nast, 1943), rinsed in water, and bleached in Stockwell's solution (Johansen, 1940). Cleared and bleached leaves were then rinsed in water, stained with 1 percent safranin, dehydrated through an ethanol series, and mounted on slides with balsam or permount mounting medium. Available stem material was prepared in the same manner in order to examine nodal anatomy in unsectioned material. A complete record of specimens examined, including their collection numbers and locations, is presented in *Appendix 1* of the original thesis (Rury, 1976). The cleared leaves examined in this study are located in the Cleared Leaf Collection, Division of Paleobotany, Smithsonian Institution (under the supervision of Leo J. Hickey, Curator), and in the collections of G. Ledyard Stebbins (University of California at Davis) and the present authors.

Illustrations of leaf venation were prepared using several techniques. Camera lucida drawings were made using a Wild dissecting microscope with a drawing attachment in order to illustrate accurately the basic and high order venation patterns of the leaf specimens. Negative prints of leaf venation patterns (see Dilcher, 1974) were prepared for several of the larger leaf specimens. In this technique, permanent slides of cleared specimens are used as negatives in a photographic enlarger to produce photographic (negative) prints of the venation patterns. Photomicrographs are also included to illustrate certain aspects of high order venation.

A limited number of specimens were paraffin-embedded and sectioned with a rotary microtome in order to study aspects of laminar anatomy.

For most species, numerous collections were examined to determine overall leaf size and morphology. Average leaf sizes were determined, in most cases, by measuring at least twenty leaves per species. Both young and mature leaves were measured to obtain a representative range of leaf size for each species studied. Published data of leaf sizes (Bentham, 1863; Hoogland, 1951; Hotchkiss, 1954; Willis, 1972) were also considered in assigning leaf size classes. Leaf size classes were designated according to the classification of Raunkiaer (1934): L. S. 1 — Leptophyll (up to 25 sq. mm.); L. S. 2 — Nanophyll (25 to 225 sq. mm.); L. S. 3 — Microphyll (225 to 2025 sq. mm.); L. S. 4 — Mesophyll (2025 to 18,222 sq. mm.).

For ease of comparison, species were considered in the taxonomic framework established by Gilg and Werdermann (1925) (APPENDIX 1). Leaf venation terminology follows, with necessary additions and modifications, the leaf architectural classification of Hickey (1973).

RESULTS

The great diversity of leaf venation patterns present within the genus *Hibbertia* can be conveniently arranged into a series of three basic types and nine subtypes. This leaf venation classification is based upon: (1) basic venation pattern; (2) details of basic venation pattern; (3) high order venation pattern; and (4) leaf size and nodal anatomy. The variability in leaf size and marginal configuration, as observed within several species of *Hibbertia*, emphasizes the necessity of careful collecting procedures in order to provide an accurate representation of the leaf morphology of any taxon.

TYPE I. SLENDER BROCHIDODROMOUS VENATION (e.g., PLATES III, F–I; IV, A, C, D, G; V, B; VI, G, I, K; XI, C).

Twenty-eight of the species examined possess a slender, weakly brochidodromous pattern designated as Type I venation. This type of leaf venation possesses slender or moderate secondary veins which generally follow a sinuous course and delimit intercostal areas of slightly irregular or relatively regular size and shape. Distinct intramarginal veins are lacking. High order venation may be lacking but is abundant in the leaves of most species. Leaves with sparse venation are reduced in size (L. S. 1, 2) and possess such xeromorphic features as a dense tomentum and revolute margins. The majority of species, however, possess abundant high order venation of the ramified, random reticulate type. Composite intersecondary veins are commonly formed by the anastomoses of admedially and transversely ramified tertiary veins. Intramarginal loop-forming veins are common in the leaves of most species and often enclose a random reticulum of veinlets. Marginal ultimate venation may be completely or in-

completely looped. Tertiary veins generally arise at wide acute angles from the secondaries and their brochidodromous arches and may ramify to form a random reticulum of indistinct vein orders (Types IB1 and IB2) or to form a system of large, polygonal "tertiary areoles" which exhibit no preferred orientation within the intercostal areas (Type IB3). Type IB3 leaf venation may also possess "pseudopercurrent" tertiary veins which are formed by transversely ramified veins that interconnect the secondary veins. Vein orders in all species are indistinct above the tertiary level, and areolation is generally incomplete and/or imperfect with freely terminating veinlets. These veinlets are simple or branched and may, as in the leaves of *H. huegelii*, possess terminal tracheoidal idioblasts. Leaves exhibiting polygonal tertiary areoles and occasional pseudopercurrent tertiaries are generally microphyllous in size, while leaves which lack these venation features are generally smaller in size, being leptophylls and nanophylls. All leaves are associated with trilacunar, three-trace nodes.

The slender, weakly brochidodromous vein pattern of *Hibbertia*, with numerous intramarginal loops and random reticulate high order venation, is similar to the leaf venation of the Magnoliidae, which has been described as "festooned brochidodromous" by Hickey and Wolfe (1975). The slight irregularity of the secondary veins, the random nature of the tertiary veins, and the occasionally poor distinction of tertiary veins from secondaries suggest that this Type I venation of *Hibbertia* is comparable to that of some plants with so-called second rank leaves (e.g., *Austrobaileya*) as described by Hickey (1971b).

TYPE I. . . . Slender, weakly brochidodromous venation lacking a strong, distinct pair of intramarginal veins. Low order venation is generally irregular or regular in its course. High order venation is generally ramified, random reticulate with poorly developed areolation.

1. High order venation is sparse or absent. Composite intersecondary veins are also sparse or absent. Leaves are reduced in size, being leptophylls or nanophylls (up to 225 sq. mm.) and often exhibiting xeromorphic features (i.e., dense pubescence, revolute margins). . . . . TYPE 1A.

TRILACUNAR SPECIES: *H. stellaris.*
UNILACUNAR SPECIES: *H. enervia, H. fasciculata, H. virgata.*

1. High order venation present and generally abundant. Composite intersecondary veins are common. High order venation usually ramified, random reticulate with incomplete and/or imperfect areolation. Leaves of various sizes and with xeromorphic features in several species. . . . . TYPE IB.

2. Percurrent and pseudopercurrent (transversely ramified) tertiary veins are absent. Tertiary and high order venation is random reticulate.

3. Leaves mostly reduced in size, being leptophylls, nanophylls, or small microphylls (few spp.). . . . . TYPE IB1.

TRILACUNAR SPECIES: *H. diffusa*, *H. glaberrima*, *H. glomerosa*, *H. huegelii*, *H. miniata*, *H. pachyrrhiza*, *H. potentilliflora*, *H. racemosa*, *H. salicifolia*, *H. subvaginata*.

UNILACUNAR SPECIES: *H. angustifolia*, *H. procumbens*.

3. Leaves not reduced in size, being microphylls (225–2025 sq. mm.). ..... TYPE IB2.

TRILACUNAR SPECIES: *H. amplexicaulis*, *H. cunninghamii*, *H. longifolia*.

2. Percurrent tertiary veins absent. Pseudopercurrent, transversely ramified tertiary veins may be present. Ramified tertiary veins form a system of large, polygonal tertiary areoles. High order venation is random reticulate with incomplete and/or imperfect areolation with numerous freely terminating veinlets. Leaves are mostly microphylls or small mesophylls (225–18,222 sq. mm.). ..... TYPE IB3.

TRILACUNAR SPECIES: *H. dentata*, *H. mylnei*, *H. nymphaea*, *H. perfoliata*, *H. pilosa*, *H. saligna*, *H. scandens*, *H. scandens* var. *oxyphyllum*, *Hibbertia* sp. 2.

TYPE II. STOUT BROCHIDODROMOUS VENATION
(e.g., PLATES I; II; V, G–I; VI, C–F, H, L–N; VII, C; VIII, IX, A, B, D–G; X; XII, F–H).

Fifty-six of the species studied possess leaves that exhibit a stout, strongly brochidodromous venation pattern, arbitrarily designated as a Type II organization. Leaves of this type possess stout secondaries which follow a straight or sinuous course and delimit intercostal areas of irregular (Type IIA) or regular (Type IIB) size and shape. The arch segments of the brochidodromous secondaries are incorporated into a pair of stout, linear (Type IIA) or scalloped (Type IIB) intramarginal veins. The intramarginal veins of unilacunar species terminate basally as a massive accumulation of tracheary elements (see PLATES VIII, A, B, H; XIII, B), whereas those of the trilacunar species fuse with the lateral leaf traces within the leaf base. Species that lack abundant high order leaf venation are designated as Type IIA1 and are unique in their possession of "transversely composite intercostal veins." Such veins are formed by the anastomoses of a few secondary and tertiary veins that follow a longitudinal course proximal and parallel to the massive, primary midvein (e.g., *H. acicularis*). Leaves having this vein pattern are all reduced in size, being leptophylls or nanophylls, and exhibit xeromorphic features.

Most Type II species, however, possess abundant high order venation that forms a ramified, random reticulum of veinlets. Tertiary veins arise at wide acute to slightly obtuse angles, from the secondary veins and their

brochidodromous arches, and exhibit various ramifications which anastomose to form composite intersecondary veins within the intercostal areas. Loop-forming veins commonly enclose a system of admedially ramified veinlets. Marginal ultimate venation is generally incomplete but may form a completely looped, fimbrial, marginal ultimate vein as in the leaves of *H. cistifolia*. Areolation is generally incomplete in the reduced leaves of the unilacunar species. Leaves exhibit variously ramified tertiary and higher order veins which form a random reticulum of incomplete and/or imperfect areoles. However, the leaves of several New Caledonian species with scalloped intramarginal veins possess a nearly orthogonal reticulum of very well-developed, nearly perfect areoles (e.g., *H. lucens*, *H. wagapii*). Vein orders are generally indistinct above the tertiary or quaternary level, and freely terminating veinlets commonly range from simple to profusely branched as in *H. trachyphylla*. Veinlets are devoid of terminal, tracheoidal idioblasts. All leaves of Type IIA designation, with linear intramarginal veins, are reduced in size, possess xeromorphic features, and are associated with unilacunar, one-trace nodes. Leaves with Type IIB designation and scalloped intramarginal veins, however, may be nanophylls associated with unilacunar, one-trace nodes, or microphylls and mesophylls associated with trilacunar, three-trace nodal patterns.

The venation patterns considered here represent two relative levels of organization. Both species with linear intramarginal veins and those with scalloped intramarginal veins have relatively regular secondary veins and random reticulate high order venation with incomplete areolation. These leaf venation patterns could be considered comparable to the second rank leaves described by Hickey (1971b). The species with scalloped intramarginal veins and an orthogonal reticulum of well-developed areoles (e.g., *H. lucens*, *H. wagapii*), however, would be more comparable to the third rank leaves of Hickey (1971b) with respect to the greater regularity of their tertiary venation. The strong intramarginal veins of these species appear, as suggested by Hickey and Wolfe (1975) of *Hibbertia* and other dicotyledonous leaves, to have originated by the fusion and strengthening of the secondary brochidodromous arches. The festooned brochidodromous venation pattern, as observed in the Type I hibbertias and within the Magnoliidae (Hickey & Wolfe, 1975), is also evident in the more regular, stout venation of these hibbertias with scalloped intramarginal veins (Type IIB). The intramarginal veins of these hibbertias exhibit different degrees of linearity which may be considered as departures from the basically "scalloped" nature of the brochidodromous arch as represented in the weakly brochidodromous leaf venation of numerous hibbertias.

TYPE II. . . . Stout brochidodromous venation with a pair of stout, distinct, linear or scalloped intramarginal veins. Composite intersecondary veins may be present. High order venation, when present, forms a ramified, random reticulum or a nearly orthogonal reticulum with incomplete or moderately well developed areolation.

1. Strong, linear intramarginal veins are present which generally terminate basally in the lamina as a mass of tracheary elements or an anastomosis of veinlets. Secondary veins are regular or irregular in their course, generally delimiting intercostal areas of irregular size and shape. TYPE IIA.

    2. High order venation sparse or absent. Composite intersecondary veins are also absent. "Transversely composite intercostal veins" are formed by secondary and a few tertiary vein anastomoses. Areolation is lacking or incomplete and poorly developed, with few high order veins. Leaves are reduced in size, being leptophylls or nanophylls with xeromorphic features. ..... TYPE IIA1.

        UNILACUNAR SPECIES: *H. acicularis*, *H. cistiflora*, *H. elata*, *H. exutiacies*, *H. stricta*.

    2. High order venation abundant, composite intersecondary veins are present, and "transversely composite intercostal veins" are absent. High order venation is ramified, random reticulate. Areolation is either incomplete and poorly developed or is nearly complete and moderately well developed. Leaves are reduced in size, being leptophylls or nanophylls usually with xeromorphic features. ..... TYPE IIA2.

        UNILACUNAR SPECIES: *H. aurea*, *H. gracilipes*, *H. hypericoides*, *H. microphylla*, *H. mucronata*, *H. pedunculata*, *H. pungens*, *H. rhadinopoda*, *H. stirlingii*, *H. tomentosa*, *H. uncinata*, *H. vestita*.

1. Strongly brochidodromous venation with a pair of stout, distinct, scalloped intramarginal veins which, in the trilacunar species, fuse basally with the lateral leaf traces. These intramarginal veins may, in the unilacunar species, terminate freely and massively within the leaf base. The trilacunar species have leaves with three leaf traces which remain distinct and unfused for several millimeters within the leaf base. The low order (2°) veins are generally very regular, delimiting intercostal areas of regular size and shape. Composite intersecondary veins are common. Pseudopercurrent, transversely ramified tertiary veins are occasionally present. High order venation is ramified, random reticulate or may be nearly orthogonal reticulate. Areolation is imperfect and nearly incomplete or is well developed and nearly perfect, often with numerous freely ending veinlets. Leaves are of various sizes, but are mostly nanophylls, microphylls, or small mesophylls. The smallest leaves are generally associated with unilacunar nodal patterns. ..... TYPE IIB.

    TRILACUNAR SPECIES: *H. altigena*, *H. baudouinii*, *H. brongniartii*, *H. coriacea*, *H. dealbata*, *H. deplancheana*, *H. ebracteata*, *H. heterotricha*, *H. inconspicua*, *H. lucens*, *H. lucida*, *H. nana*, *H. ngoyensis*, *H. oubatchensis*, *H. pancheri*, *H. patula*, *H. podocarpifolia*, *H. pulchella*, *H. scabra*,

H. tontoutensia, *H. trachyphylla*, *H. vanieri*, *H. virotii*, *H. wagapii*, *Hibbertia* sp. 1, *Hibbertia* sp. 3.

UNILACUNAR SPECIES: *H. aspera*, *H. asterotricha*, *H. bracteata*, *H. cistoidea*, *H. cistifolia*, *H. furfuracea*, *H. hermanniifolia*, *H. hexandra*, *H. melhanoides*, *H. nitida*, *H. oblongata*, *H. sericea*, *H. silvestris*.

TYPE III. CRASPEDODROMOUS VENATION
(e.g., PLATES IV, E, F; VI, A; VII, B, D; IX, C; XI, A, B).

Craspedodromous leaf venation occurs in only thirteen of the species examined. All but one of these species possess either a semicraspedodromous or a mixed craspedodromous venation pattern which is associated with a toothed or half-toothed leaf margin. The craspedodromous condition appears, in most cases, to be the result of an ontogenetic modification of the weakly brochidodromous pattern. Semicraspedodromous venation has apparently resulted from the formation and subsequent vascularization of marginal teeth in leaves with weakly brochidodromous venation. The tooth vasculature arises exmedially from the brochidodromous arch in leaves of *Hibbertia cuneiformis*, *H. linearis*, *H. linearis* var. *obtusifolia*, and *H. serrata*. This ontogenetic transition will be considered in more detail later. Such a morphological leaf dimorphism of entire-margined young leaves and toothed older leaves has been illustrated for *H. serrata* by Hotchkiss (1954); a similar example is illustrated for *H. linearis* var. *obtusifolia* in PLATE XI, A.

As in the leaves of species with weakly brochidodromous venation, semicraspedodromous leaves also possess slender or moderate secondary veins which diverge from a moderate midvein at moderately acute angles and follow a sinuous and recurved (*H. montana* var. *major*) or curved (*H. linearis* var. *obtusifolia*) course, delimiting intercostal areas of relatively irregular size and shape which commonly enclose composite intersecondary veins. Abundant loop-forming veins arise exmedially from the brochidodromous arches and form a festooned brochidodromous vein pattern similar to that of the species with entire leaf margins and a Type I venation pattern. Occasional pseudopercurrent tertiary veins can be found, and a system of large, polygonal "tertiary areoles," with no preferred orientation within the intercostal areas, may occur. Tertiary areoles are subdivided into a random reticulum of admedially and transversely ramified veinlets. There may also be ramified high order veins within the intramarginal loops. High order venation of the semicraspedodromous leaves is essentially identical to that of the weakly brochidodromous, Type I leaves of several species of *Hibbertia*. Marginal ultimate venation is generally incompletely looped and may be of tertiary or quaternary origin. Areolation is generally incomplete and/or imperfect and ramified, with freely ending veinlets that may bear terminal idioblasts (e.g., *H. linearis* var. *obtusifolia*).

Simple craspedodromous venation was observed only in the immature and mature leaves of *H. grossulariifolia*. This species possesses moderate, nearly straight secondaries which diverge from the moderate midvein at consistently moderate acute angles, delimit intercostal areas of very uniform size and shape, and terminate in marginal teeth of the dillenioid type (*sensu* Hickey & Wolfe, 1975). Composite intersecondaries arise via admedially ramified tertiary veins which in turn originate, admedially, from geniculate, transversely ramified ("pseudopercurrent") tertiaries. Large, polygonal tertiary areoles of non-preferred orientation are subdivided, by variously ramified high order veins and veinlets, into a random reticulum of incomplete areoles. Numerous freely ending veinlets with terminal idioblasts are common. With respect to high order venation, the leaves of *H. grossulariifolia* are very similar to the majority of plants with semicraspedodromous and weakly brochidodromous venation.

The mixed craspedodromous venation pattern is present in *H. banksii* and *H. holtzei*. In the mature leaves of *H. banksii*, this pattern appears to be the result of an ontogenetic transition from a weakly brochidodromous condition. Young leaves of *H. banksii* have an entire margin and a weakly brochidodromous venation pattern with a nearly orthogonal reticulum of very well-developed, small, quadrangular areoles. Larger, more mature leaves, however, have an entire margin and a weakly brochidodromous pattern only within the basal half of the lamina. The upper half of the lamina possesses a crenate margin that is associated with vein termini from several simple craspedodromous secondary veins. The high order venation exhibits an identical pattern in both the immature and mature leaves of *H. banksii*. The ontogenetic change in basic venation pattern is illustrated in PLATE VII, B, D. The areolation of leaves of *H. banksii* represents the highest level of development in *Hibbertia* and is comparable to that of *Hibbertia* sp. 1 (PLATE XV, C), a species to which it is believed to be closely related (Stebbins, 1975, pers. comm.). Freely ending veinlets and terminal tracheoidal idioblasts are absent in the leaves of *H. banksii*.

The mixed craspedodromous leaves of *H. holtzei* possess a basal eucamptodromous pattern and an apical simple craspedodromous pattern. The leaf is crenate along its upper half, with hydathodal crenations supplied directly by the simple craspedodromous secondary veins. Basal, upcurving eucamptodromous secondary veins follow a sinuous, tapering course and form a series of intramarginal loops along the exmedial sides of the tenuous, superadjacent secondary veins. Composite intersecondary veins and large, polygonal tertiary areoles with non-preferred orientation are formed by admedial and transverse tertiary vein ramifications. The tertiary areoles are subdivided into a random reticulum of high order veins and veinlet termini. Percurrent tertiary and pseudopercurrent tertiary veins are common, the former being most abundant between the basal, eucamptodromous secondary veins. Tertiary veins generally arise at right angles but may arise at wide acute or slightly obtuse angles. Loop-forming veins are numerous and form up to five (2° to 6°) orders of intramarginal loops which commonly enclose a random reticulum of ad-

medially ramified, high order veinlets. Marginal ultimate venation is mostly completely looped and of quaternary or quintary origin. Vein orders are indistinct above the tertiary level and are variously ramified into a random reticulum of imperfect, moderately well-developed areolation. Simple or slightly branched, freely terminating veinlets are commonly devoid of terminal idioblasts.

The leaves of all craspedodromous species are microphylls or mesophylls and are associated with trilacunar, three-trace nodes. The three leaf traces may remain distinct and unfused within a sessile leaf base (semicraspedodromous species) or may fuse within the base of a laminar (*H. grossulariifolia*) or terete (*H. banksii*, *H. holtzei*) petiole to form a single primary midvein. The leaves of species with these three types of craspedodromy appear to correspond to a level of structural organization slightly below the third rank condition as described by Hickey (1971b).

TYPE III. . . . Leaves with craspedodromous venation patterns. Secondary veins generally follow a straight or irregularly sinuous course and delimit intercostal areas which are relatively regular in size and shape. Secondary veins are occasionally interconnected by pseudopercurrent, transversely ramified tertiary veins. High order veins form a ramified, random reticulum with incomplete and/or imperfect areolation. High order venation may also form a nearly perfect system of small, quadrangular areoles (*H. banksii*). Leaves are large nanophylls, microphylls, or small mesophylls. . . . . 1.

1. Basic venation pattern is semicraspedodromous or mixed craspedodromous with vascularized marginal teeth, at least along the upper half of the leaf margin. An ontogenetic change from a weakly brochidodromous vein pattern is evident in the species with a semicraspedodromous, mature venation pattern. High order venation is generally ramified, random reticulate with incomplete areolation. High order venation may be more nearly orthogonal reticulate with moderately developed (*H. holtzei*) or well-developed areolation (*H. banksii*). . . . . TYPE IIIA.

TRILACUNAR SPECIES: *H. banksii*, *H. cuneiformis*, *H. gilgiana*, *H. holtzei*, *H. lasiopus*, *H. linearis*, *H. linearis* var. *obtusifolia*, *H. montana*, *H. montana* var. *major*, *H. quadricolor*, *H. serrata*, *H. tetrandra*.

1. Basic venation pattern is simple craspedodromous throughout ontogeny. Secondary veins are straight and regular, and delimit intercostal areas of regular size and shape. Marginal teeth are directly vascularized by these secondaries. Pseudopercurrent tertiary veins are present. High order venation is ramified, random reticulate with incomplete and imperfect areolation. . . . . TYPE IIIB.

TRILACUNAR SPECIES: *H. grossulariifolia*.

DISCUSSION

ONTOGENETIC TRANSITIONS.

Ontogenetic changes in basic leaf venation pattern are apparent in several species of *Hibbertia*. Weakly brochidodromous patterns are associated with entire margins in all species examined. However, in several species entire margins and an associated weakly brochidodromous venation are confined to the smaller leaves. More mature, larger leaves possess a toothed margin and a semicraspedodromous venation pattern which apparently results from the formation of marginal teeth vascularized by veins arising exmedially from the slender brochidodromous, secondary arches of the developing leaves. The resultant semicraspedodromous venation pattern is identical to the weakly brochidodromous leaf venation exhibited by the juvenile foliage in all respects except the vascularized, marginal teeth. It remains unclear whether the apparent ontogenetic transition of leaf morphology and venation occurs within a single leaf or within series of successively younger leaves along the branches of these plants; further studies are clearly necessary.

However, the marginal ultimate venation of several species with weakly brochidodromous venation indicates that this "transition potential" may reside within individual leaves. Leaves of *H. amplexicaulis*, *H. cunninghamii*, and *H. perfoliata* have massive tracheary accumulations within their marginal ultimate venation adjacent to scarcely noticeable marginal bulges (see PLATE XIV, D). These tracheary masses are considered by Stebbins (1976, pers. comm.) to be identical to the tooth vasculature of the dentate-leaved hibbertias. These tracheary accumulations may represent a "pre-tooth" and thus may indicate a potential of several species to form toothed leaf margins. The occurrence of marginal teeth in open, semi-xeric habitats seems to favor this hypothesis since marginal teeth do not seem to be disadvantageous in these drier areas, but may simply represent an ontogenetic development in response to periodic rainfall and ephemerally moist conditions.

Another possibility is to consider these tracheary accumulations as relictual teeth. Since the species exhibiting this feature are inhabitants of mesic regions, there seems to be no obvious active selective pressure which would favor the loss of marginal teeth. Hence, if these structures are, indeed, relictual teeth, it might be reasonable to postulate a recent migration of these species from a dry region into more mesic habitats.

Leaves of *Hibbertia banksii* apparently represent a different type of ontogenetic change in basic venation pattern. The young leaves of this species possess a weakly brochidodromous vein pattern with tertiary and high order veins that are poorly distinguished from one another and from the secondary veins. The transition, in the upper half of the leaf, from this weak brochidodromy to simple craspedodromy apparently results from a differential thickening of high order veins which connect the basal portion of the brochidodromous secondary arch with the marginal tooth.

The arch segments in the upper half of the leaf evidently become "de-emphasized" with respect to their development and become part of the high order, intercostal vein reticulum. Apparently, an extension of the secondary vein develops from high order veins and connects the base of the brochidodromous arch with the marginal crenation to form a simple craspedodromous secondary vein. Such a "shift" in vein development is responsible, in many dicot leaves, for ontogenetic transitions from semi-craspedodromy to simple craspedodromy (Hickey, 1975, pers. comm.). As in the ontogenetic transitions observed in other species, the high order venation of leaves of *H. banksii* remains unchanged throughout their ontogeny. This evidence seems to indicate a morphological continuum between the weakly brochidodromous and the craspedodromous venation patterns which appears to be ontogenetically and developmentally traversed by the leaves of several species of *Hibbertia*.

The relationship between the formation and vascularization of marginal teeth or denticulations is of great interest both developmentally and physiologically. The occurrence of marginal "pre-teeth," as in the leaves of *H. amplexicaulis*, *H. cunninghamii*, and *H. perfoliata*, suggests a possible hormonal mechanism in the "co-formation" of marginal teeth and tooth vasculature. Massive tracheary accumulations are often found within protuberant leaf apices (see PLATE XV, A), as in the marginal teeth, and suggest a possible apical growth for the marginal teeth. Two preliminary hypotheses of hormonal activity at these sites of tooth formation may warrant further investigation: (1) acropetal transport of a tooth-formation stimulus from the vascular aggregations; and (2) basipetal transport of a vascularization stimulus from the meristematic, marginal tooth apex. The presence of a massive accumulation of tracheary tissue not associated with a marginal tooth in the leaves of several species (e.g., *H. cunninghamii*) would seem to favor the former hypothesis. A detailed developmental-physiological investigation is needed to confirm or negate these hypotheses.

NODAL ANATOMY, LEAF SIZE, AND LEAF ATTACHMENT.

Nodes of *Hibbertia* are either trilacunar, three-trace, or unilacunar, one-trace. Sixty-two species studied possess trilacunar, three-trace nodes, and such nodes usually occur in species with sessile leaves. Fifty-one of these trilacunar species have leaves that are either microphyllous or mesophyllous in size. Furthermore, the majority of these species have three unfused leaf traces within a sessile leaf base. This correlation between leaf size and nodal pattern is not absolute, however, since species with reduced leptophyllous or nanophyllous leaves do, occasionally, possess trilacunar, three-trace nodes (e.g., *H. diffusa*). Eleven of the trilacunar species examined have reduced, leptophyllous or nanophyllous leaves, but most of the species examined that possess reduced leaves lack a trilacunar, three-trace nodal pattern. Trilacunar, three-trace nodes are considered to be the primitive, or generalized, condition in *Hibbertia* and the entire family Dilleniaceae (Dickison, 1969; Stebbins, 1972). The occurrence of

this generalized nodal pattern in the majority of species is not unusual since *Hibbertia* is the most primitive or generalized genus of the entire family Dilleniaceae with respect to other morphological features (viz., large flowers with spirally arranged parts and free carpels, primitive wood anatomy, and sessile leaves with relatively unspecialized venation patterns (Dickison, 1967a, 1968)). The frequent association of trilacunar nodes with unfused leaf traces within the sessile bases of relatively large leaves suggests that nodal anatomy, leaf size, and leaf attachment may represent a complex of characters that have closely interrelated and interdependent character states.

Trilacunar nodes are also found in association with clasping, sheathing, or perfoliate leaf bases in *H. amplexicaulis*, *H. nymphaea*, and *H. perfoliata*, the leaves of which are all microphylls and exhibit weakly brochidodromous venation patterns.

Several species of *Hibbertia* also possess petiolate microphylls or mesophylls that are associated with trilacunar, three-trace nodes. The leaf traces fuse within the base of the laminar (*H. grossulariifolia*) or terete (*H. coriacea*, *H. dentata*) petiole to form a single primary midvein. The petiolate condition probably represents a morphological advancement since it is observed in the more advanced, trilacunar (*Tetracera*) and multilacunar (*Davilla*, *Dillenia*) genera of Dilleniaceae, all of which also have relatively large, microphyllous or mesophyllous leaves (Dickison, 1969). Mutilacunar nodes, which in the Dilleniaceae are considered to be derived from the primitive, trilacunar condition (Dickison, 1969), are strongly correlated (100 percent) with large leaf sizes and the presence of petioles.

Thirty-five of the species examined possess unilacunar, one-trace nodes that are generally associated with sessile leaves. Nearly all of these unilacunar species also have reduced, leptophyllous or nanophyllous leaves. A strong reciprocal correlation is evident in that ca. 74 percent of the species with reduced leaves also possess unilacunar, one-trace nodal patterns. These correlations are a reflection of the relationship between leaf size and nodal anatomy in *Hibbertia*. A similar correlation is apparent in the dilleniaceous genus *Pachynema*, which illustrates the same association of reduced, scalelike leaves with unilacunar, one-trace nodal patterns. The reduction in leaf size and nodal structure has been considered a specialization within the Dilleniaceae, derived from the generalized, trilacunar condition (Dickison, 1969; Stebbins, 1972).

Venation patterns of the laminar base are also related to nodal structure, regardless of leaf size. In trilacunar species with both weakly and strongly brochidodromous leaf venation, the basal secondary veins often diverge from the lateral leaf traces within the sessile leaf base (e.g., *H. gilgiana*, *H. virotii*). The unilacunar species of *Hibbertia* generally possess reduced leaves with strongly brochidodromous venation and stout, linear (Type IIA) or scalloped (Type IIB) intramarginal veins which terminate massively within the sessile leaf bases on either side of the single massive midvein (see PLATES VI, H; VIII, A, H; XIII, B). The intramarginal vein termini remain distinct from the midvein and may anasto-

mose with numerous veins and veinlets to form a dense, basal reticulum of tracheary elements as in *H. sericea*. Such basal intramarginal vein termini are always associated with unilacunar, one-trace nodes, regardless of leaf size. The structural and physiological significance of these massive vein termini is uncertain.

Leaf venation in relation to the systematics of Hibbertia.

Sections Trisema, Polystiche, Spicatae, subsection Trimorphandra of sect. Cyclandra, and several species of uncertain taxonomic position are exclusively New Caledonian or Fijian in distribution. All of these New Caledonian and Fijian species possess large leaves, trilacunar, three-trace nodes, and a remarkably similar, strongly brochidodromous Type IIB venation pattern. These species differ only with respect to their high order venation, which may be distinctly ramified and random reticulate with incomplete areolation (e.g., *H. lucida*, *H. trachyphylla*), or less distinctly ramified and nearly orthogonal reticulate with very well-developed areolation as in the leaves of *H. lucens* and *H. wagapii*. Terminal idioblasts are lacking in the leaves of all New Caledonian and Fijian hibbertias, and the species groupings (*sensu* Gilg & Werdermann, 1925) appear to be quite natural on the basis of vegetative morphology. On the basis of both leaf venation and floral morphology (see Appendix 1), however, subsect. Trimorphandra would be more naturally placed in one of these New Caledonian sections than in the Australian section Cyclandra.

Section Cyclandra, which is primarily Australian except for the aforementioned New Caledonian subsect. Trimorphandra, represents a very heterogeneous assemblage of leaf venation patterns (see Table 1). This section includes those hibbertias with the most generalized leaf venation, as well as the most generalized floral structure, within the genus (see Appendix 1). Both unilacunar and trilacunar species are present and are associated with either normal sized (L. S. 3, 4) or reduced leaves (L. S. 1, 2). Seventeen species possess leaves with a weakly brochidodromous venation pattern, whereas fourteen species exhibit strongly brochidodromous leaf venation. Craspedodromous leaf venation occurs in only seven of the species examined from this section, the majority of which exhibit the semicraspedodromous pattern.

Several of the subsections of Cyclandra, however, exhibit a relatively homogeneous assemblage of leaf venation patterns (Table 1). All seven species examined from subsect. Tomentosae, for example, possess leaves with strongly brochidodromous venation. Subsection Hemihibbertiae is somewhat less homogeneous; the leaf venation of eight of the twelve species examined is weakly brochidodromous; that of the other four species is either strongly brochidodromous or craspedodromous. However, considering the similarity of the weakly brochidodromous and semicraspedodromous leaf venation patterns, the total array of venation patterns within this subsection is relatively homogeneous. Subsection Subsessiles represents the most heterogeneous grouping as evidenced by the presence of four different leaf venation patterns (see Table 1). Subsection Brac-

TABLE 1. **Distribution of venation types among sections of the genus Hibbertia (sensu Gilg & Werdermann, 1925).***

SECTION	VENATION TYPES								
	IA	IB1	IB2	IB3	IIA1	IIA2	IIB	IIIA	IIIB
TRISEMA							+		
POLYSTICHE							+		
SPICATAE							+		
CYCLANDRA	+	+	+	+	+	+	+	+	+
FASCICULATAE	+	+							
BRACTEATAE	+	+						+	
SUBSESSILES		+		+	+			+	
BRACHYANTHERAE	+					+			
VESTITAE						+			
TOMENTOSAE						+	+		
HEMIHIBBERTIAE		+	+	+			+	+	+
TRIMORPHANDRA							+		
SALICIFOLIAE		+							
CANDOLLEA	+	+				+		+	
HEMIPLEURANDRA						+	+		
HEMISTEMMA	+						+	+	
PLEURANDRA	+			+	+	+	+		
Uncertain			+				+	+	

* Based on the examination of 97 species.

TEATAE, on the other hand, is a relatively homogeneous grouping having consistently weakly brochidodromous leaf venation or a slight modification thereof. Subsections FASCICULATAE, BRACHYANTHERAE, and VESTITAE, each with few species, are also relatively uniform with respect to leaf morphology.

Most species of the section CANDOLLEA have leaf venation patterns of the weakly brochidodromous type and possess trilacunar, three-trace nodes. This section thus represents a natural species grouping on the basis of both vegetative and floral morphology (see APPENDIX 1).

Sections HEMIPLEURANDRA and PLEURANDRA are very homogeneous with respect to leaf venation patterns and include species with uniformly unilacunar, one-trace nodes and reduced leaves with strongly brochidodromous venation patterns. All of the species studied also have basal intramarginal vein termini (see PLATE VII, A, H).

Hibbertia section HEMISTEMMA includes a relatively heterogeneous array of leaf venation patterns with strongly brochidodromous venation (*H. coriacea*, *H. dealbata*, *Hibbertia* sp. 1), mixed craspedodromous venation (*H. banksii*, *H. holtzei*), and reduced leaves with weakly brochidodromous venation (*H. angustifolia*). The single character state common to all species of this section except *H. angustifolia* is the well-developed high order venation with nearly complete areolation.

It can be concluded that, with few exceptions, the subgeneric groups

established by Gilg and Werdermann (1925) on the basis of floral morphology generally represent natural associations with respect to the homogeneity of vegetative characters and leaf venation patterns.

Evolutionary trends.

Relative levels of specialization of the foliar venation of woody dicotyledons have been determined through comparative morphological studies of both fossil and extant dicot leaves (Hickey, 1971b; Wolfe, 1973; Hickey & Wolfe, 1975). General trends of specialization are represented by: (1) an increase in regularity of both low and high order venation; (2) a shift from vein orders which are indistinct to successive vein orders which are readily distinguished from one another; (3) a shift from tertiary venation which is random to that which is very regular, often with rigidly percurrent veins traversing the intercostal areas; and (4) a progressive development from random, incomplete areolation to orthogonal, well-developed (perfect) areolation. The different levels of leaf venation specialization in woody dicots have been called "ranks" by Hickey (1971b) and may be outlined as follows. First rank leaves have secondary veins that follow an irregular course and delimit intercostal areas that lack uniform size and shape. Second rank leaves possess secondary veins that are relatively regular in their course, intercostal areas of generally uniform size and shape, and random tertiaries that are frequently not well differentiated from the secondaries. Third rank leaves exhibit more organized venation, with tertiaries of relatively consistent course and areoles of random size or placement. Fourth rank leaves are further specialized, with areoles of uniform size and shape that are regularly arranged within the intercostal areas.

Several of the above levels, or "ranks," of leaf venation specialization occur in *Hibbertia*. The basic venation pattern of all species is pinnate brochidodromous or craspedodromous and, thus, may be considered as generally primitive (*sensu* Hickey & Wolfe, 1975) in comparison to woody dicotyledons as a whole. Simple leaves with entire margins, as present in most species of *Hibbertia*, are considered the primitive leaf type in woody dicots (Hickey & Wolfe, 1975).

Species of *Hibbertia* with weakly brochidodromous leaf venation and random reticulate high order venation represent the least specialized venation in the genus and also in the entire family Dilleniaceae. The relative irregularity of the secondary veins, the intercostal areas, and the high order venation is that of the first, or in some cases (e.g., *H. amplexicaulis*) second rank leaves (*sensu* Hickey, 1971b). The irregular venation of such Type IB1 leaves (e.g., *H. glaberrima*, *H. glomerosa*) presents the most probable condition for the leaf venation of the ancestral Dilleniaceae. Approximately 30 percent of the species studied occur in mainland Australia (including Tasmania) and have such first or low second rank leaf venation.

Leaves of *Hibbertia* with strong, regular brochidodromous venation with distinct intramarginal veins and ramified, random reticulate or nearly or-

thogonal reticulate (e.g., *H. lucida, H. wagapii*) high order venation exhibit second or third rank organization (*sensu* Hickey, 1971b).

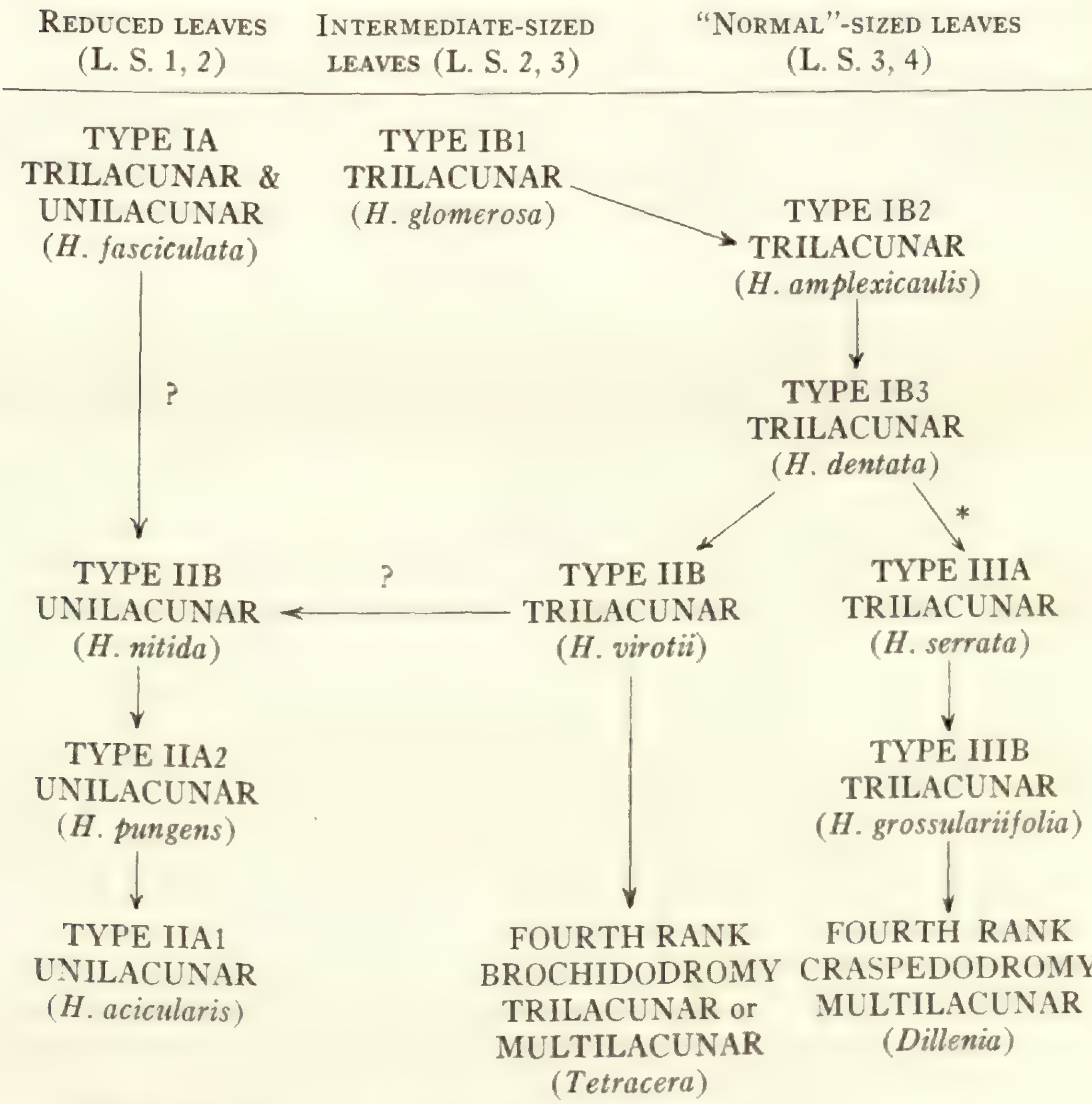
Craspedodromous species of *Hibbertia* are more specialized than the brochidodromous species with respect to their toothed marginal configuration, which is regarded as an advanced feature. However, the majority of these species have vein patterns that are no more advanced than those of species with weakly brochidodromous venation. Most craspedodromous hibbertias have a semicraspedodromous venation of first or second rank organization. The mixed craspedodromous leaves of *H. banksii* and *H. holtzei*, however, are considerably more advanced than the semicraspedodromous species with respect to their high order venation. *Hibbertia banksii* has a well-developed system of small, quadrangular areoles, a condition which is lacking in species with a semicraspedodromous venation. Leaves of *H. holtzei* have a moderately specialized system of high order venation that contains several percurrent tertiary veins and a moderately well-developed system of areoles. The simple craspedodromous leaves of *Hibbertia grossulariifolia* are advanced over most hibbertias with respect to their crenate margins. The regularity of the secondary veins and of the intercostal areas of this species represents a basic vein pattern which is more specialized than that of species with a weakly brochidodromous condition. The high order veins, however, with the exception of a few weakly percurrent tertiary veins, are organized into a ramified, random reticulum of incomplete areoles which is no more advanced than in other species.

Hibbertia has the least specialized leaf venation in the Dilleniaceae. All other genera in the family, except the xerophytic genus *Pachynema*, have a very regular eucamptodromous-brochidodromous, brochidodromous, or simple craspedodromous venation pattern with a moderately or well-developed system of rigidly percurrent tertiary venation and oriented, nearly perfect, or perfect areolation. Rigidly percurrent tertiary venation and oriented, well-developed areolation are lacking in all hibbertias. Hickey (1971a) has observed that variations from the basic venation pattern within a family may appear in disjunct genera or in genera that are found in environments atypical of the remainder of the family. Most genera of Dilleniaceae inhabit mesic, everwet parts of the tropics (Hoogland, 1951), whereas *Hibbertia* favors habitats that range from xeric to mesic-hydric with numerous species inhabiting semi-xeric regions. The apparent "regression" to a lower level of foliar venation in numerous needle-leaved species of *Hibbertia*, as compared to the other second and third rank hibbertias, presents an excellent example of Hickey's observation. A similar situation is illustrated by the genus *Pachynema*, which is usually regarded as an extreme xeromorphic derivative of *Hibbertia* and exhibits a "regression" of leaf venation specialization below the level characteristic of *Hibbertia* and all other Dilleniaceae. Hickey's (1971b) contention that plants native to arctic, alpine, and arid environments may also show such a regression is supported by evidence from the xeric species of *Hibbertia* and the xeric genus *Pachynema*. In dealing with taxa of extreme habitats, however, great difficulty is encountered in assigning relative levels of specializa-

tion to foliar venation patterns. The reductions in the degree of leaf vascularization of some needle-leaved *Hibbertia* species and of *Pachynema* are, in fact, specializations of a type not represented by Hickey's four evolutionary ranks of leaf venation. It is more accurate to refer to such "underdeveloped" leaf venation patterns as being morphological divergences rather than morphological regressions, since among reduced, xeromorphic leaves it is impossible to determine relative levels of specialization of venation (*sensu* Hickey, 1971b). The relative homogeneity of leaf venation patterns present in most genera of Dilleniaceae and the extreme heterogeneity of leaf venation of *Hibbertia* appear to be products resulting from adaptive radiation within different environments.

An evolutionary series of leaf and leaf venation types, based upon relative levels of vegetative morphological specialization observed within *Hibbertia* and other genera, is postulated for the entire family Dilleniaceae in CHART 1.

CHART 1. **Evolutionary trends of leaf venation patterns of Dilleniaceae.**


REDUCED LEAVES (L. S. 1, 2)
INTERMEDIATE-SIZED LEAVES (L. S. 2, 3)
"NORMAL"-SIZED LEAVES (L. S. 3, 4)
TYPE IA TRILACUNAR & UNILACUNAR (H. fasciculata)
TYPE IB1 TRILACUNAR (H. glomerosa)
TYPE IB2 TRILACUNAR (H. amplexicaulis)
TYPE IB3 TRILACUNAR (H. dentata)
?
*
TYPE IIB UNILACUNAR (H. nitida)
?
TYPE IIB TRILACUNAR (H. virotii)
TYPE IIIA TRILACUNAR (H. serrata)
TYPE IIA2 UNILACUNAR (H. pungens)
TYPE IIIB TRILACUNAR (H. grossulariifolia)
TYPE IIA1 UNILACUNAR (H. acicularis)
FOURTH RANK BROCHIDODROMY TRILACUNAR or MULTILACUNAR (Tetracera)
FOURTH RANK CRASPEDODROMY MULTILACUNAR (Dillenia)

* Occurs ontogenetically in several species of *Hibbertia*.

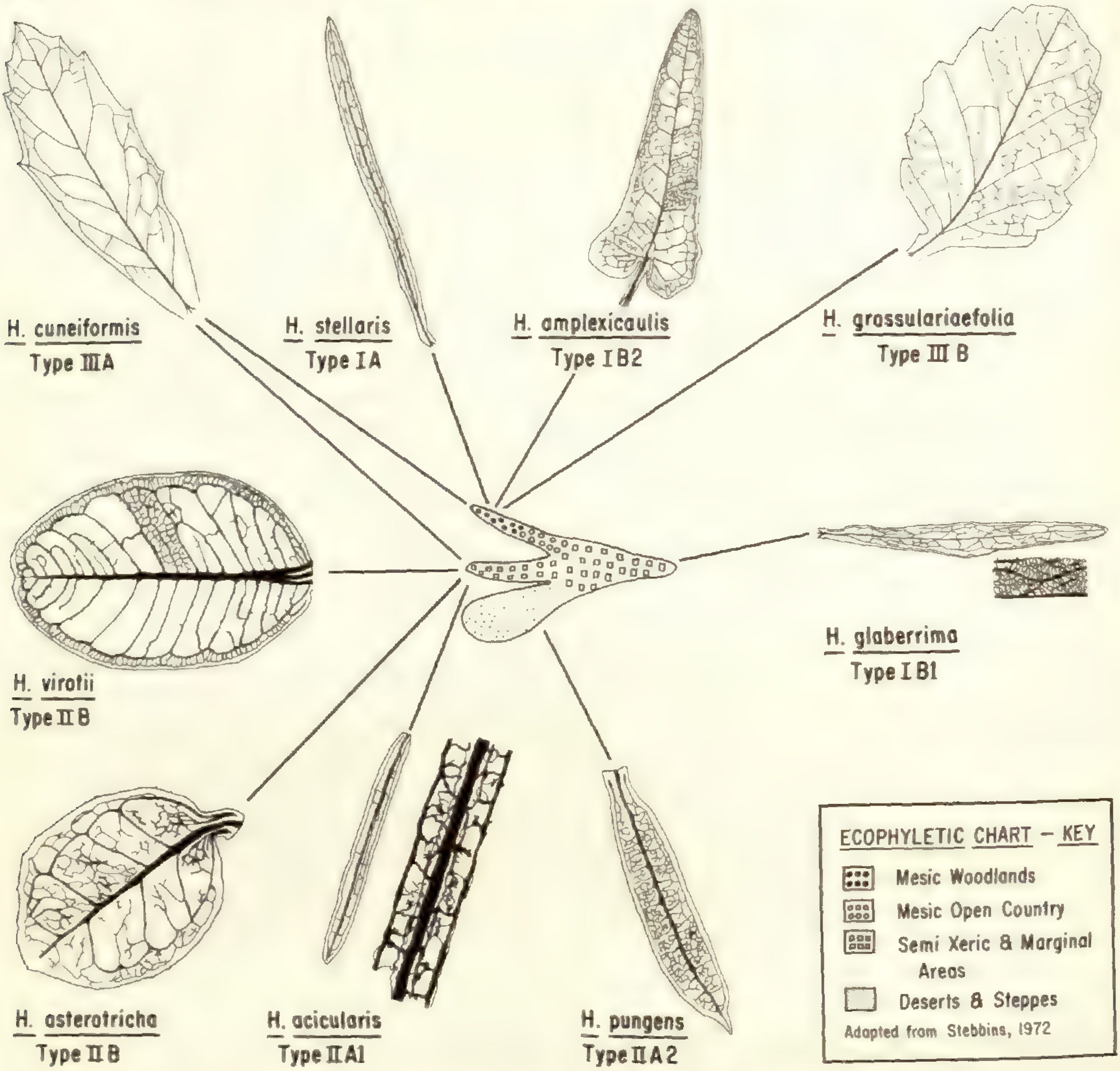


FIGURE 1. Adaptive radiation and leaf venation of *Hibbertia*. (Adapted from Stebbins with permission from the author and publisher.)

ADAPTIVE RADIATION WITHIN THE DILLENIACEAE.

Generalized habitat data, assembled for species of *Hibbertia* and for the other genera of Dilleniaceae, are employed in considerations of the structural diversification within *Hibbertia* and the entire family Dilleniaceae. Detailed information about their microhabitats and microclimatic preferences was not available. The morphological diversity of leaf venation patterns is illustrated in conjunction with the presumed patterns of adaptive radiation as envisioned by Stebbins (1972) for *Hibbertia* (FIGURE 1) and for the entire family (FIGURE 2).

Adaptive radiation, as defined by Radford *et al.* (1974, p. 543), is "evolutionary diversification within a group of related species or other taxa brought about by adaptations to different selective forces through time or migration." Stebbins (1974) has considered this phenomenon at some length and outlines several adaptations which generally occur in response to environmental conditions. Adaptations commonly selected for by drought or cold are: (1) reduction in growth, and therefore in size, of a plant;

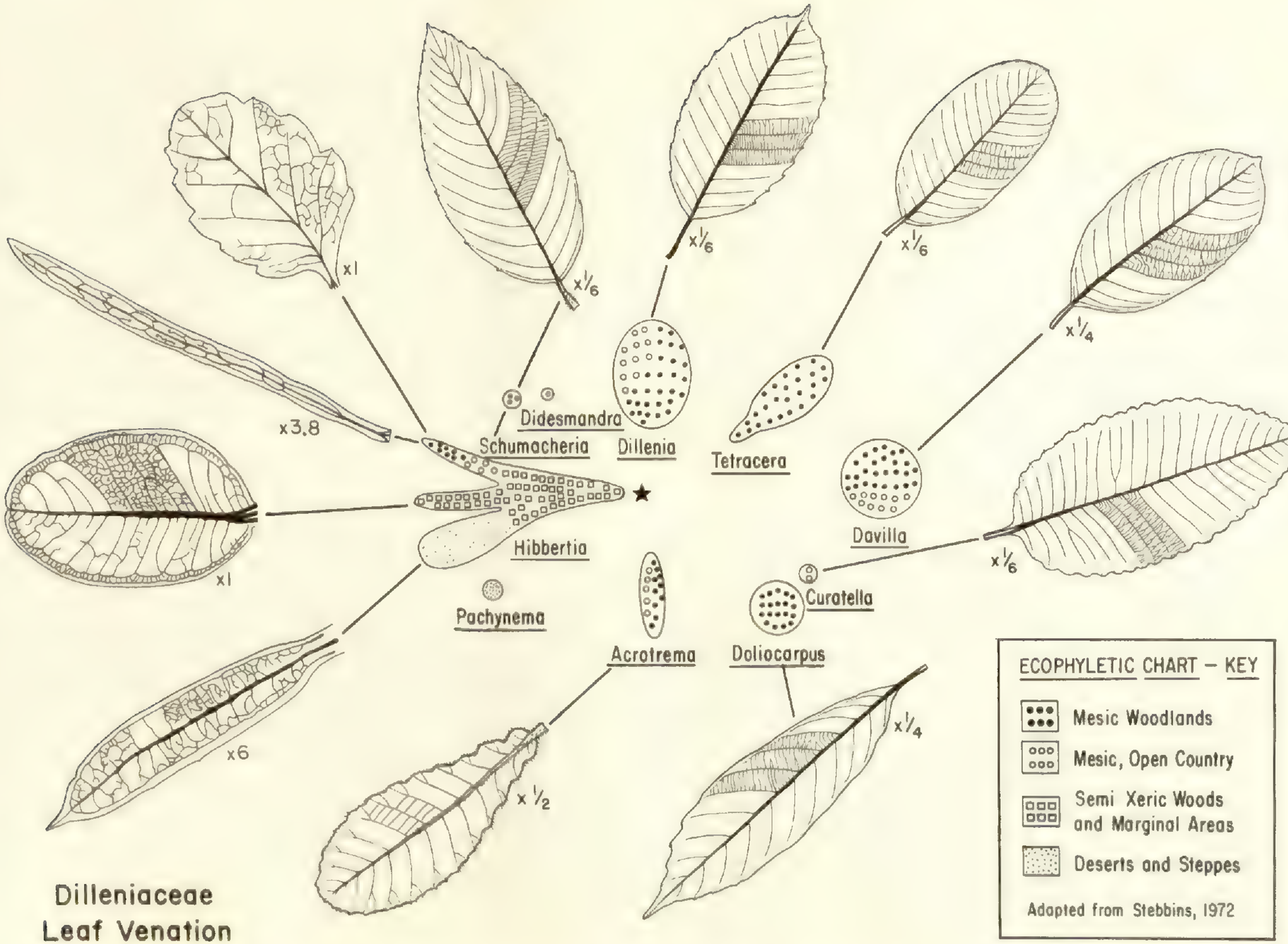


FIGURE 2. Adaptive radiation and leaf venation of Dilleniaceae. (Adapted from Stebbins with permission.)

(2) acquisition of physiological specializations; (3) hormonal adjustments to coordinate flowering with favorable seasons; and (4) reductions in growth that result in condensations of floral structure in response to the shortening of the favorable flowering-fruiting season. Conversely, Stebbins also outlined several changes that are fostered by an improving environment: (1) increased growth vigor and resultant increased plant size; (2) production of more and larger seeds; and (3) an increase in the number of potential animal pollinators.

Stebbins (*loc. cit.*) proposed a semi-xeric origin for the Dilleniaceae from which there was adaptive radiation into all habitats presently occupied by dilleniaceous taxa. The genus *Hibbertia*, which exhibits its greatest morphological diversity within such habitats (FIGURE 1), supports Stebbins's hypothesis concerning the original habitat of the Dilleniaceae. This correlation of extreme morphological diversity within semi-xeric habitats is also illustrated by the Dilleniaceae at the generic level. *Hibbertia* is both the most ecologically widespread and the most morphologically diverse genus of the family.

The reduced plant size of many hibbertias and all species of *Pachynema* is a response to the harsh, xeric habitats in which they occur. The reduced plant habit has also resulted in reduced leaf size in all xeric and numerous semi-xeric species of *Hibbertia*, as well as in the species of the xeric genus *Pachynema*. Reduced leaf size is an ecological adaptation which minimizes leaf surface area, thus retarding water loss and surface heating, enabling the plant to withstand prolonged drought seasons. The hibbertias and pachynemas of both semi-xeric and xeric habitats experience seasonal drought as do numerous other plants of the Australian "sclerophyll communities" (Specht, 1963). Leaf size reduction has been accompanied in *Pachynema* and numerous species of *Hibbertia* by the acquisition of other xeromorphic foliar features such as woolly vestiture, revolute margins, and stomatal crypts, all of which are extremely rare in the leaves of mesic species. Such reduced, xeromorphic leaves have been noted by Carlquist (1974) to be exceedingly common in plants of southwestern Australia, a region where numerous species of *Hibbertia* occur. Leaf venation patterns of xeric species commonly exhibit massive primary and intramarginal veins, massive intramarginal vein termini within the leaf base, and areolation that is lacking or poorly developed (see PLATES III, B, C; VI, C). The "regressions" in leaf venation organization exhibited by these hibbertias of extreme habitats are commonly observed in many woody dicotyledons growing in such environments (Hickey, 1971b). Reductions in overall leaf size have apparently resulted in a relatively massive primary vein as compared to leaf width. The similarity of leaf venation patterns among both small- and large-leaved *Hibbertia* species suggests that leaf size is a more variable character than is the pattern of leaf venation. The experimental induction of leaf expansion in various small-leaved Australian taxa, through the addition of phosphorous to pot cultures, also indicates that leaf size is a much more plastic, environmentally controlled character than is leaf venation (Beadle, 1968). It appears, therefore, that numerous

xerophytic species of *Hibbertia* have adapted "along the path of least resistance" (*sensu* Stebbins, 1974) through a reduction in leaf growth and expansion, rather than a rearrangement or reduction, of the leaf procambial network. Reductions in nodal anatomy from the generalized, trilacunar condition to the specialized, unilacunar condition have also occurred. Trilacunar, three-trace nodal patterns do not occur in xeric species of *Hibbertia*; conversely, unilacunar nodes are very rare in the mesic species. Numerous hibbertias and all species of *Pachynema* exhibit reductions in the number of perianth parts that are apparently a response to seasonal drought, an adaptation considered common for angiosperms in general (Stebbins, 1974).

Numerous morphological changes that commonly accompany plant radiation into more favorable habitats are illustrated by many species of *Hibbertia* and by all mesic genera of the Dilleniaceae. Morphological changes that have accompanied such a radiation are present in the mesic Australian species of *Hibbertia* and in the hibbertias that inhabit the more equable island habitats of New Caledonia, New Guinea, Fiji, and Madagascar. Increased plant size and vigor have resulted in the formation of large rosette trees of the New Caledonian hibbertias. Increased growth vigor is also evident in the mesic, lianoid taxa *Hibbertia scandens* and the genera *Davilla* and *Tetracera*. The arboreal growth habit of *Dillenia*, a mesic Old World genus, illustrates the favorable effect of mesic habitats upon plant growth. The mesomorphic condition of the foliage of all mesic dilleniaceous genera and of most mesic species of *Hibbertia* is also correlated with an adaptive radiation into more favorable mesic habitats. The largest leaved forms of *Hibbertia*, for example, occur as rosette trees in New Caledonia. These species (e.g., *H. baudouinii*) commonly inhabit moist montane regions of this equable island habitat and exhibit steady transpiration rates and vessel diameters comparable to those of mesic, woody dicots (Carlquist, 1975). Leaf mesomorphy is also striking in other mesic genera of Dilleniaceae (e.g., *Dillenia*, *Tetracera*) that possess large microphyllous or mesophyllous leaves. The differentiation of distinct petioles has also accompanied adaptive radiations into more mesic habitats. All petiolate species of *Hibbertia* (e.g., *H. banksii*, *H. coriacea*, *H. dentata*) and most petiolate genera of Dilleniaceae inhabit mesic regions and/or equable island habitats such as New Caledonia, New Guinea, or Madagascar, whereas petiolate leaves do not occur in xeric species. The more specialized petiolate condition, accordingly, appears to have arisen only within mesic habitats in dilleniaceous taxa. *Curatella*, however, a petiolate genus that inhabits open areas which are drier than areas inhabited by genera such as *Dillenia* and *Tetracera*, possesses pentalacunar nodes, well-developed petioles, and toothed leaves with fourth rank, simple craspedodromous venation. The presence of these vegetative specializations which are commonly restricted to mesic dilleniaceous taxa suggests that *Curatella* has experienced a secondary radiation from mesic habitats into more xeric, open areas. The absence of xeromorphic features, such as woolly vestiture and revolute leaf margins, is also evident in the leaves

of mesic genera and species of Dilleniaceae. Strong intramarginal veins, a specialization that presumably strengthens the leaf, occur in leaves of several species which inhabit islands with relatively equable climates (e.g., *H. coriacea* of Madagascar; all New Caledonian and Fijian species). The possession of "pre-teeth" (e.g., *H. cunninghamii*) and vascularized marginal teeth are features of leaf morphology generally restricted to mesic genera and species. Marginal teeth of the dillenioid type (Hickey & Wolfe, 1975), most common in the mesic species of *Hibbertia* and also in the genera *Curatella*, *Dillenia*, *Didesmandra*, and *Tetracera*, probably serve a hydathodal function.

The occurrence of reduced leaves in several mesic or hydric species of *Hibbertia* (e.g., *H. salicifolia*, *H. stellaris*, *H. stirlingii*) represents an exception to the general occurrence of microphylly and mesophylly in the mesic habitat. This may represent leaf-size reductions in response to an extreme, hydric habitat, or secondary migrations of xeromorphic species into a mesic-hydric habitat where their xeromorphic characters are not disadvantageous.

Increased specialization in leaf venation has also accompanied the adaptive radiation of numerous hibbertias and other dilleniaceous genera into more favorable habitats. The best-developed leaf venation of *Hibbertia*, for example, occurs in species from equable island habitats such as *H. banksii* from New Guinea, *H. coriacea* from Madagascar, and *H. lucens* from Fiji and New Caledonia. The contention of Hickey and Doyle (1972b) that evolutionary increase in the regularity of vein orders of woody dicot leaves has progressed from low order to high order veins is supported by the leaves of *H. grossulariifolia* and numerous New Caledonian species. These plants possess leaves with very regular low order (secondary) veins but exhibit much less regularity in their high order venation. Leaves of other mesic dilleniaceous genera, however, are quite specialized in their possession of very regular low and high order venation, a highly specialized system of rigidly percurrent tertiary venation, and a well-developed system of areoles (see PLATE XII). A system of percurrent tertiary veins has been interpreted to be an advanced feature of amentiferous leaves (Wolfe, 1973), and an advanced feature of highly specialized, "fourth rank" leaves of woody dicotyledons in general (Hickey, 1971b). The occurrence of terminal idioblasts in the leaves of many mesic hibbertias (e.g., *H. grossulariifolia*, *H. linearis*) is a striking contrast to the condition found by Sehgal and Paliwal (1974) in the leaves of *Euphorbia*, where idioblasts occur only in the xeric species. The significance of terminal idioblasts in the leaves of mesic hibbertias in unclear. Nodal anatomy has apparently undergone an amplification from the primitive trilacunar condition to an advanced multilacunar condition in all mesic genera of Dilleniaceae except *Hibbertia* and *Tetracera* (Dickison, 1969). A summary of the morphological features acquired by dilleniaceous taxa during their ancient adaptive radiations is presented in TABLE 2.

TABLE 2. **Summary of morphological characteristics that have resulted from adaptive radiations within the family Dilleniaceae.**

XERIC RADIANTS

1. Reductions in leaf size (*Hibbertia* and *Pachynema*).
2. Development of xeromorphic anatomical leaf features.
3. "Regression" in level of specialization of leaf venation patterns.
4. Development of a massive primary vein and massive intramarginal veins in the reduced leaves.
5. Reduction in nodal pattern to a unilacunar, one-trace condition with which massive, basal intramarginal vein termini are associated.
6. Decrease in plant size and growth vigor.
7. Overall reductions in floral morphology and anatomy, including reduced seed production per flower.

MESIC RADIANTS

1. Development of larger leaves (L. S. 3, 4) with well-developed petioles with three or more fused leaf traces.
2. Development (in numerous cases) of marginal, dillenioid teeth and very regular, simple craspedodromous venation in the leaves.
3. Development of a rigidly percurrent tertiary vein system enclosing a system of well-developed areolation in the leaves.
4. Amplification of trilacunar nodes to a multilacunar condition in mesic genera other than *Hibbertia* and *Tetracera*.
5. Increase in plant size and growth vigor.
6. Reduction in carpel number and number of ovules per carpel.
7. Increase in carpel and/or ovule number in several cases.
8. Amplification of stamen number, presumably in response to coleopteran pollination.
9. Development of various degrees of basal or lateral syncarpy.

CONCLUSIONS

1. The extreme diversity of leaf morphology and venation patterns of *Hibbertia* has resulted from radiation into and evolution within a wide range of ecological situations.
2. Numerous species of *Hibbertia* exhibit ontogenetic changes in leaf morphology and basic venation pattern. These changes, however, do not alter the high order vein configuration from the original juvenile condition.
3. The greatest diversity of leaf morphology and venation occurs within the Australian hibbertias.
4. New Caledonian hibbertias, which exhibit remarkably similar venation patterns, appear to be more variable in their floral structure than in their leaf morphology and venation.
5. The subgeneric sections of *Hibbertia* (*sensu* Gilg & Werdermann, 1925) generally constitute natural species assemblages on the basis of leaf morphology.
6. Several levels of evolutionary advancement in the organization of leaf venation are evident in species of *Hibbertia*.

7. Leaf venation patterns of some species of *Hibbertia* are the most unspecialized of the entire family Dilleniaceae.
8. Evolutionary trends in leaf morphology and venation, observed within *Hibbertia* and other genera of Dilleniaceae, are generally correlated with evolutionary trends observed elsewhere in the plant body.
9. Features of leaf morphology and venation of *Hibbertia* reveal vegetative character syndromes that are correlated with habitat.
10. Regressions in the level of organization of leaf venation below that characteristic of the genus are evident in the leaves of numerous hibbertias of extreme xeric or hydric habitats.
11. The best-developed leaf venation patterns generally occur in hibbertias of equable island habitats such as Fiji, Madagascar, New Caledonia, and New Guinea.
12. Ecophyletic specializations observed within species of *Hibbertia* closely parallel those observed, at the generic level, within the Dilleniaceae as a whole.

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Appendix 1. Intrageneric treatment of Hibbertia Andrews (sensu Gilg and Werdermann, 1925).

Section Trisema (Hooker) Gilg (ca. 10 species). New Caledonia. Inflorescence spicate. Sepals 5; petals 3 or 4; stamens numerous (50 to 100), encircling the single, terminal carpel; staminodia absent; carpel glabrous with 8 to 12 ovules. Species studied: *H. deplancheana* Bur. ex Guillaumin, *H. lucida* Bur. ex Guillaumin, *H. oubatchensis* Schltr., *H. pancheri* (Brongn. & Gris) Briq., *H. patula* Guillaumin, *H. vanieri* Beauvis., *H. wagapii* Gilg.

Section Polystiche Baker (ca. 2 species). New Caledonia. Inflorescence spicate. Sepals 5; petals 5; stamens numerous (100+) encircling 3 or 4 carpels; staminodia absent; carpels glabrous with 15 or more ovules. Species studied: *H. baudouinii* Brongn. & Gris.

Section Spicatae Baker (ca. 10 species). New Caledonia, Fiji. Inflorescence a secund spike. Sepals 5; petals 5; stamens numerous (65 to 100), encircling a pair of carpels; staminodia absent; carpels glabrous with 10 ovules each. Species studied: *H. altigena* Schltr., *H. brongniartii* Gilg, *H. lucens* Brongn. & Gris ex Seb. & Pancher, *H. ngoyensis* Schltr., *H. podocarpifolia* Schltr., *H. scabra* Brongn. & Gris, *H. trachyphylla* Schltr., *H. virotii* Guillaumin.

Section Cyclandra F. Mueller ex Gilg (ca. 50 species). Australia and New Caledonia. Floral structure is highly variable. Flowers pentamerous with numerous stamens surrounding the carpels on all sides.

Subsection Fasciculatae Bentham (ca. 2 species). New South Wales, South Australia, Tasmania, and Victoria. Flowers sessile. Sepals 5; petals 5; stamens fasciculate, up to 20 in number; staminodia absent; carpels glabrous, 3 to 5, with 6 to 8 ovules each. Species studied: *H. fasciculata* R. Br. ex DC., *H. procumbens* (Labill.) DC.

Subsection Bracteatae Bentham (ca. 6 species). New South Wales, southwestern Australia, Tasmania, and Victoria. Flowers sessile. Sepals 5; petals 5; stamens 10 to 20 or 30 to 60; staminodia absent; carpels glabrous, 3 or 5, with 1 or 2 ovules each. Species studied: *H. miniata* Gardner, *H. montana* Steudel, *H. montana* var. *major* Steudel, *H. pilosa* Steudel, *H. serrata* Hotchkiss, *H. virgata* R. Br. ex DC.

Subsection Subsessiles Bentham (ca. 7 species). East Australia, southeast Australia, New South Wales, Queensland, and Victoria. Flowers sessile-terminal or axillary. Sepals 5; petals 5; stamens 15 to 30; staminodia absent; carpels 3, glabrous, with 1 or 2 ovules each. Species studied: *H. diffusa* R. Br. ex DC., *H. elata* Maiden & Betche, *H. linearis* R. Br. ex DC., *H. linearis* var. *obtusifolia* DC., *H. saligna* R. Br. ex DC., *H. scandens* (Willd.) Gilg, *H. scandens* var. *oxyphyllum* Domin.

Subsection Brachyantherae Bentham (ca. 3 species). Southwest Australia. Flowers pedunculate. Sepals 5; petals 5; stamens 11 to 20; staminodia absent; carpels glabrous, 3 or 5; with 1 or 2 ovules each. Species studied: *H. pungens* Bentham, *H. stellaris* Endl.

Subsection Vestitae Bentham (ca. 3 species). East and southeast Australia. Flowers sessile or pedunculate. Sepals 5; petals 5; stamens 15 to 30 or more; staminodia present or absent; carpels 3, villous, with 4 to 6 ovules

each. Species studied: *H. pedunculata* R. Br. ex DC., *H. vestita* A. Cunn. ex Bentham.

Subsection TOMENTOSAE Bentham (ca. 10 species). North Australia, northeast Australia, east Australia, and southeast Australia. Flowers axillary-pedunculate. Sepals 5; petals 5; stamens 6 to 50 or more; staminodia few or absent; carpels 2, tomentose, with 1 to 3 ovules each. Species studied: *H. cistifolia* R. Br., *H. hermanniifolia* DC., *H. hexandra* C. T. White, *H. melhanoides* F. Mueller, *H. oblongata* R. Br. ex DC., *H. stirlingii* C. T. White, *H. tomentosa* R. Br.

Subsection HEMIHIBBERTIAE Bentham (ca. 14 species). Central Australia, east Australia, northwest Australia, and southwest Australia. Flowers pedunculate. Sepals 5; petals 5; stamens 20 to 200; staminodia present; carpels glabrous (except *H. grossulariifolia* and *H. lasiopus*), 3, 5, or 8 to 15, with 2 to 8 ovules each. Species studied: *H. amplexicaulis* Steudel, *H. cunninghamii* Hooker, *H. dentata* R. Br. ex DC., *H. gilgiana* Diels, *H. glaberrima* F. Mueller, *H. grossulariifolia* (Salisb.) Salisb., *H. lasiopus* Bentham, *H. longifolia* F. Mueller, *H. mylnei* Bentham, *H. nymphaea* Diels, *H. perfoliata* Endl., *H. potentilliflora* F. Mueller ex Bentham, *H. quadricolor* Domin.

Subsection TRIMORPHANDRA (Brongn. & Gris) Baker (ca. 2 species). New Caledonia. Inflorescence spicate or flowers solitary, sessile. Sepals 5, petals 5, stamens numerous; staminodia present; carpels 2, glabrous, with 3 to 5 ovules. Species studied: *H. heterotricha* Bur. ex Guillaumin, *H. pulchella* (Brongn. & Gris) Schltr.

Subsection SALICIFOLIAE Gilg (one species). East Australia. Flowers axillary-sessile. Sepals 5; petals 5; stamens 10, filaments forming a tube; staminodia absent; carpels 2, glabrous and uniovulate. Species studied: *H. salicifolia* F. Mueller.

Section CANDOLLEA (Labill.) F. Mueller (ca. 12 species). Southwest Australia. Sepals 5; petals 5; stamens 10 to 35 in 5 bundles of 2 to 7 stamens each; staminodia absent; carpels 3 or 5, glabrous, with 1 to 3 ovules each.

Subsection SESSILES Gilg (ca. 8 species). Flowers axillary-sessile. Species studied: *H. cuneiformis* (Labill.) Sm., *H. enervia* (DC.) Hoogl., *H. glomerosa* (Bentham) F. Mueller, *H. huegelii* (Endl.) F. Mueller, *H. pachyrrhiza* Steudel, *H. tetrandra* (Lindley) Gilg.

Subsection PEDUNCULATAE Gilg (ca. 4 species). Flowers axillary-pedunculate. Species studied: *H. racemosa* (Endl.) Gilg, *H. subvaginata* (Steudel) F. Mueller, *H. uncinata* (Bentham) F. Mueller.

Section HEMIPLEURANDRA Bentham. Southwest Australia.

Subsection UNIFLORAE Gilg (ca. 10 species). Flowers axillary-pedunculate. Sepals 5; petals 5; stamens declinate (on one side of gynoecium), rarely more than 12; staminodia present; carpels 2, villous, with 2 to 4 ovules each. Species studied: *H. aurea* Steudel, *H. furfuracea* (R. Br. ex DC.) Bentham, *H. hypericoides* (DC.) Bentham, *H. microphylla* Steudel, *H. rhadinopoda* F. Mueller, *H. silvestris* Diels.

Section HEMISTEMMA (Juss.) Bentham (ca. 8 species). Inflorescence spicate with two or more flowers. Sepals 5; petals 5; stamens numerous (up to 50),

declinate; staminodia numerous (up to 60); declinate; carpels 2, villous, with 2 or 3 ovules each.

Subsection OPPOSITIFOLIAE Gilg (one species). Madagascar. Opposite leaf arrangement. Species studied: *H. coriacea* (Pers.) Baillon.

Subsection ALTERNIFOLIAE Gilg (ca. 7 species). New Guinea, northern Australia. Alternate leaf arrangement. Species studied: *H. angustifolia* (R. Br. ex DC.) Bentham, *H. banksii* (R. Br. ex DC.) Bentham, *H. dealbata* (R. Br. ex DC.) Bentham, *H. holtzei* F. Mueller, *Hibbertia* sp. 1.

Section PLEURANDRA (Labill.) Bentham (ca. 13 species). East Australia, southeast Australia, and Western Australia. Flowers sessile, solitary-pedunculate, or in solitary heads. Sepals 5; petals 5; stamens declinate and few, rarely more than 15; staminodia absent; carpels 2, generally villous or tomentose, with 2 to 4 ovules each.

Subsection PLATYPHYLLAE Gilg (ca. 8 species). Leaves generally small, flat, and broad. Species studied: *H. aspera* DC., *H. asterotricha* (Sieber ex Sprengel) N. A. Wakefield, *H. bracteata* (R. Br. ex DC.) Bentham, *H. cistiflora* N. A. Wakefield, *H. cistoidea* (Hooker) C. T. White, *H. nitida* (R. Br. ex DC.) F. Mueller, *H. sericea* (R. Br. ex DC.) Bentham, *H. stricta* (DC.) F. Mueller.

Subsection ACICULARES Gilg (ca. 5 species). Leaves linear and needle-like. Species studied: *H. acicularis* (Labill.) F. Mueller, *H. exutiacies* N. A. Wakefield, *H. gracilipes* Bentham, *H. mucronata* Bentham.

Section uncertain (ca. 40 species) (presently being revised by Prof. R. D. Hoogland, The Australian National University). New Caledonia and Australia. Species studied: *H. ebracteata* Bur. ex Guillaumin, *H. inconspicua* Ostf., *H. nana* Däniker, *H. tontoutensis* Guillaumin, *Hibbertia* sp. 2, *Hibbertia* sp. 3.

EXPLANATION OF PLATES

PLATE I

Leaf venation of *Hibbertia*, section TRISEMA. Scale indications represent 1 mm. A, *H. lucida* (*Baumann-Bodenheim 15829*). B, *H. oubatchensis* (*H. S. McKee 3371*). C, D, *H. deplancheana* (*R. F. Thorne 28232*).

PLATE II

Leaf venation of *Hibbertia*, sections POLYSTICHE (A) and SPICATAE (B–D). Scale indications represent 1 mm. A, *H. baudouinii* (*J. T. Buchholz 1577*). B, *H. virotii* (*R. Virot 161*). C, *H. altigena* (*H. S. McKee 3709*). D, *H. ngoyensis* (*Guillaumin & Baumann-Bodenheim 12555*).

PLATE III

Leaf venation of *Hibbertia*, section CYCLANDRA, subsections SUBSESSILES (F–I), BRACHYANTHERAE (A–C), VESTITAE (D, E). Scale indications represent 1 mm. A, *H. stellaris* (*A. M. Ashby 2007*). B, C, *H. pungens* (*Royce 7640*).

D, *H. pedunculata* (*Anon. s.n.*, A). *E*, *H. vestita* (*E. F. Constable 6382*). F–H, *H. linearis* (*C. T. White 8580*). I, *H. scandens* var. *oxyphyllum* (*NCU 423743*).

PLATE IV

Leaf venation of *Hibbertia*, section CYCLANDRA, subsection HEMIHIBBERTIAE. Scale indications represent 1 mm. A, *H. glaberrima* (*D. J. Whibley 1081*). B, *H. gilgiana* (*C. L. Wilson 856*). C, *H. dentata* (*Cult. s.n.*, K). D, *H. amplexicaulis* (*E. Pritzel 531*). E, F, *H. grossulariifolia* (*C. L. Wilson 851*). G, *H. nymphaea* (*A. Morrison s.n.*).

PLATE V

Leaf venation of *Hibbertia*, section CYCLANDRA, subsections TOMENTOSAE (A, C–F), TRIMORPHANDRA (G–I), and SALICIFOLIAE (B). Scale indications represent 1 mm. A, *H. cistifolia* (*R. L. Specht 843*). B, *H. salicifolia* (*C. L. Wilson 625*). C, *H. tomentosa* (*R. L. Specht 638*). D, E, *H. stirlingii* (*C. L. Wilson 757*). F, *H. hexandra* (*E. F. Constable 1362*). G–I, *H. pulchella* (*Franc 1597*).

PLATE VI

Leaf venation of *Hibbertia*, sections CANDOLLEA (A–C, G, I–K) and HEMIPLEURANDRA (D–F, H, L–N). Scale indications represent 1 mm. A, *H. cuneiformis* (*E. H. Wilson 297*). B, *H. pachyrrhiza* (*C. L. Wilson 861*). C, *H. uncinata* (*C. L. Wilson 155*). D, E, *H. hypericoides* (*M. H. Jones 34*). F, *H. rhadinopoda* (*E. Pritzel 97*). G, *H. racemosa* (*C. L. Wilson 811*). H, *H. microphylla* (*C. T. White 5317*). I, *H. huegelii* (*C. L. Wilson 777*). J, *H. tetrandra* (*E C3544*). K, *H. subvaginata* (*C. L. Wilson 764*). L, M, *H. aurea* (*C. L. Wilson 843*). N, *H. furfuracea* (*C. T. White 5382*).

PLATE VII

Leaf venation of *Hibbertia*, section HEMISTEMMA. Scale indications represent 1 mm. A, *H. angustifolia* (*Philson & Earle 111*). B, *H. banksii* (*L. J. Brass 8431*). C, *H. coriacea* (*H. Humbert 5866*). D, *H. banksii* (*L. J. Brass 19425*).

PLATE VIII

Leaf venation of *Hibbertia*, section PLEURANDRA. Scale indications represent 1 mm. A, *H. asterotricha* (*NCU 445391*). B, C, *H. acicularis* (*NCU 445396*). D, *H. stricta* (*T. B. Muir 2623*). E, *H. nitida* (*Fl. Novae Holl. 141*). F, *H. gracilipes* (*Royce 5792*). G, H, *H. sericea* (*E. F. Constable 3850*). I, *H. aspera* (*E. F. Constable 4311*). J, *H. mucronata* (*C. L. Wilson 792*).

PLATE IX

Leaf venation of *Hibbertia*, sections CYCLANDRA (C, F), PLEURANDRA (B, E), and uncertain (A, D, G). Scale indications represent 1 mm. A, *H. ebracteata* (*Guillaumin & Baumann-Bodenheim 11659*). B, *H. cistoidea* (*E. F. Constable 5139*). C, *H. tetrandra* (*C. L. Wilson 848*). D, G, *H. tontoutensis* (*McMillan 5060*). E, *H. cistiflora* (*S. Helms 1290*). F, *H. elata* (*R. Coveny 3737*).

PLATE X

Leaf venation of *Hibbertia*, sections CYCLANDRA (subsect. TOMENTOSAE) (A, B, E), HEMISTEMMA (D, F), and PLEURANDRA (C). A, *H. cistifolia* (*R. L. Specht 843*), × 2.4. B, *H. oblongata* (*R. L. Specht 427*), × 2.4. C, *H. bracteata* (*Anderson & Boorman s.n.*), × 2.3. D, *H. coriacea* (*H. Humbert 5866*), × 2. E, *H. melhanoides* (*C. L. Wilson 740*), × 2.3. F, *H. dealbata* (*R. L. Specht 844*), × 1.9.

PLATE XI

Leaf venation of *Hibbertia*, sections CYCLANDRA (A, C) and HEMISTEMMA (B). A, *H. linearis* var. *obtusifolia* (*Lazarides & Story s.n.*), × 2.3. B, *H. holtzei* (*US 2378199*), × 1.3. C, *H. cunninghamii* (*R. D. Royce 5774*), × 1.8.

PLATE XII

Leaf venation of Dilleniaceae. A, *Curatella americana* (*Irwin 5470*), × 2. B, *Hibbertia wagapii* (*R. F. Thorne 28266*), × 2. C, *Tetracera macrophylla* (*Cult. s.n.*, SING), × 1.7. D, *Doliocarpus major* (*MO 1245995*), × 1.8. E, *Dillenia albiflos* (*Anon. s.n.*), × 1.2. F, *Hibbertia trachyphylla* (*C. T. White 2126*), × 3. G, *Hibbertia lucens* (*A. C. Smith 1877*), × 2. H, *Hibbertia pancheri* (*Franc 2257*), × 2.

PLATE XIII

Details of leaf venation in *Hibbertia*. A, *H. aurea* (*C. L. Wilson 843*), node showing a single leaf trace, × 67. B, *H. uncinata* (*C. L. Wilson 155*), leaf base with single trace and lateral, massive intramarginal vein termini, × 63. C, *H. diffusa* (*E. F. Constable s.n.*), leaf base with three unfused traces × 50. D, *H. coriacea* (*H. Humbert 5866*), marginal ultimate leaf venation, × 67. E, *H. heterotricha* (*H. S. McKee 7753*), marginal ultimate leaf venation, × 67. F, *H. huegelii* (*C. L. Wilson 777*), intercostal leaf venation with free vein termini and idioblasts, × 67.

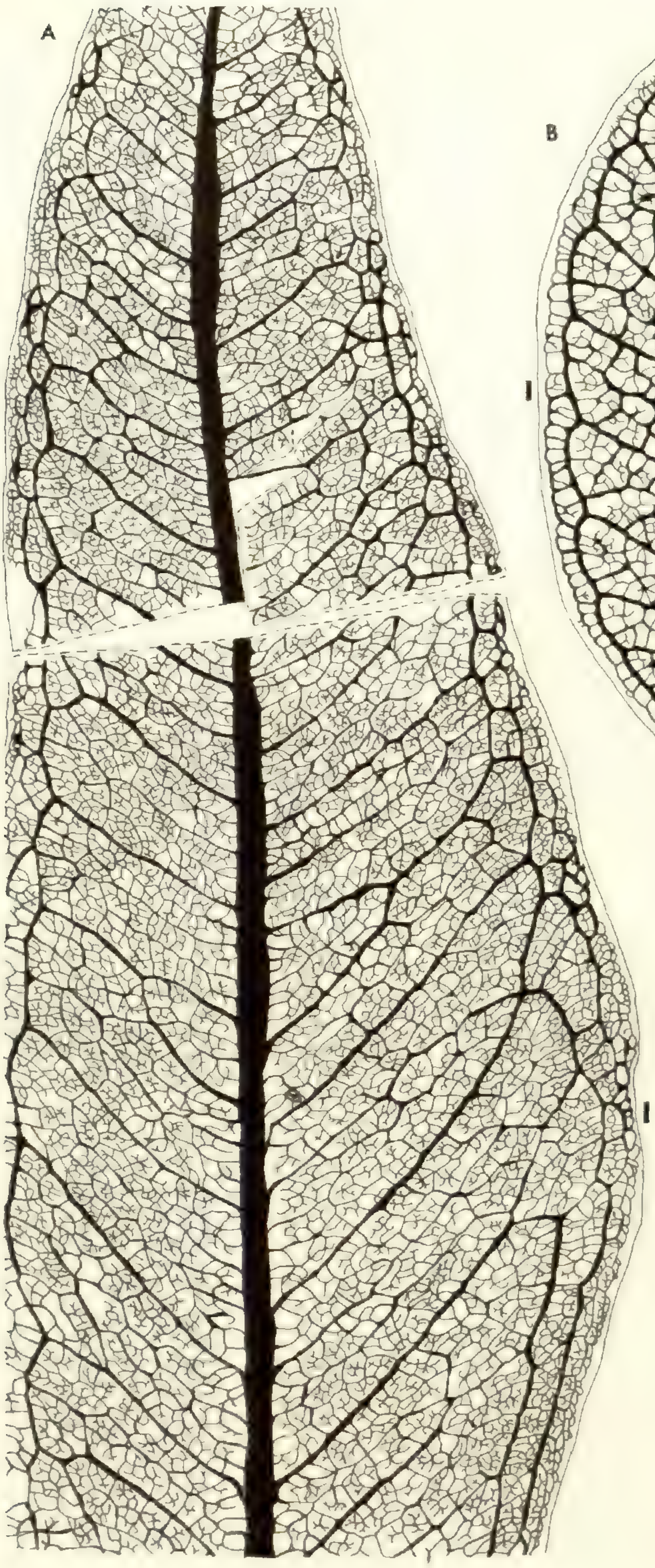
PLATE XIV

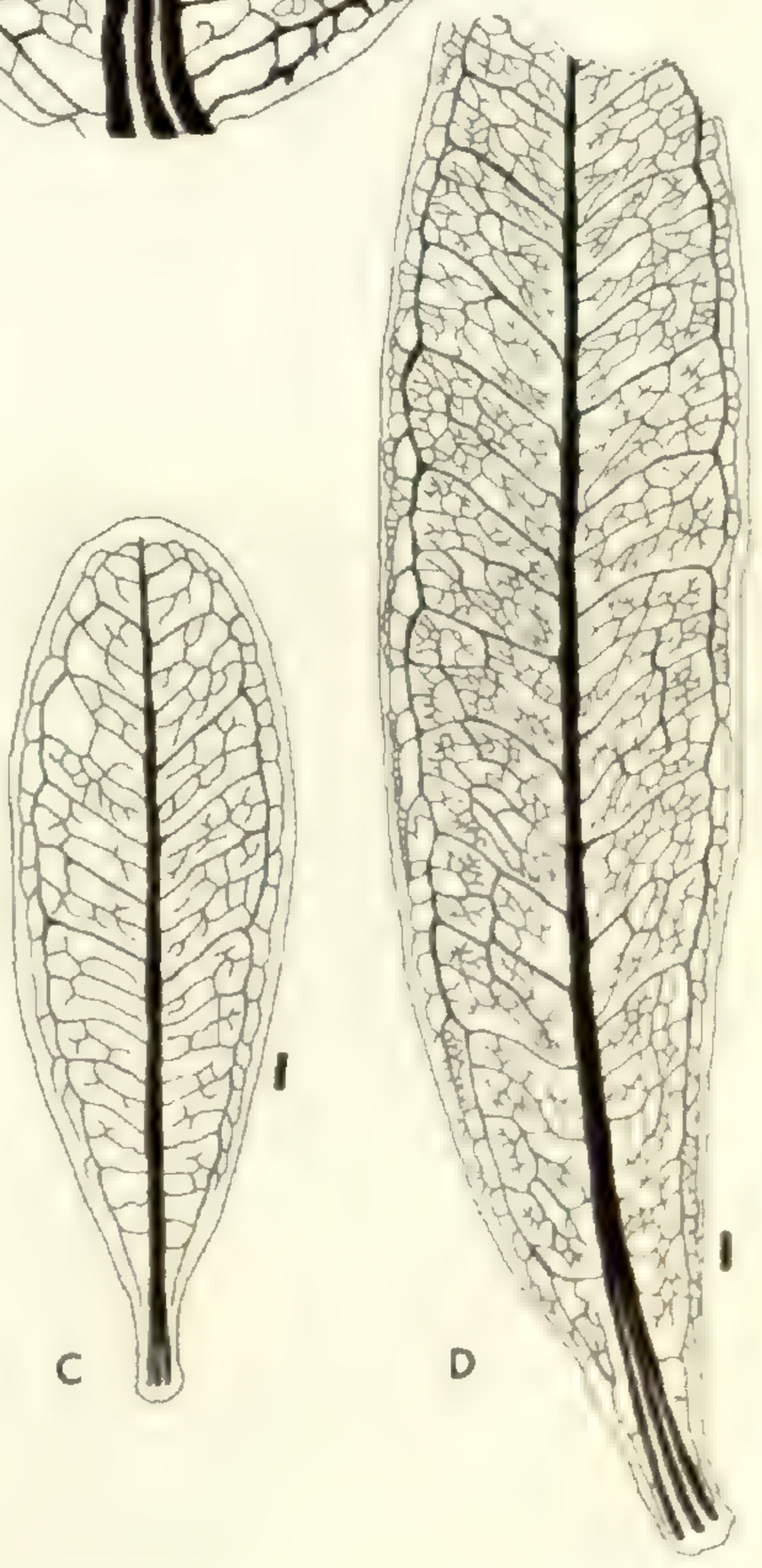
Marginal teeth of leaves of *Hibbertia*, exhibiting the dillenioid tooth structure. A, *H. cuneiformis* (*R. D. Hoogland 12536*), × 24. B, *H. grossulariifolia* (*C. L. Wilson 851*), × 76. C, *H. cuneiformis* (*Cult. s.n.*, K), × 101. D, *H. cunninghamii* (*R. D. Royce 5774*), "pretooth" of marginal ultimate venation, × 84. E, *H. linearis* var. *obtusifolia* (*Lazarides & Story s.n.*), × 168. (Photograph A courtesy of G. Ledyard Stebbins.)

PLATE XV

Details of *Hibbertia* leaf venation. A, *H. racemosa* (*C. L. Wilson 811*), note massive tracheary accumulations associated with apical-lateral teeth, × 91. B, *H. glomerosa* (*G. L. Stebbins A-5*), note irregularity of veinlets, × 16. C, *Hibbertia* sp. 1 (*Lazarides 7859*), × 2.4. D, *H. montana* (*R. D. Hoogland 12512*), note ramified intercostal veins, × 24. (Photographs B–D courtesy of G. Ledyard Stebbins.)

RURY & DICKISON, LEAF VENATION PATTERNS





RURY & DICKISON, LEAF VENATION PATTERNS

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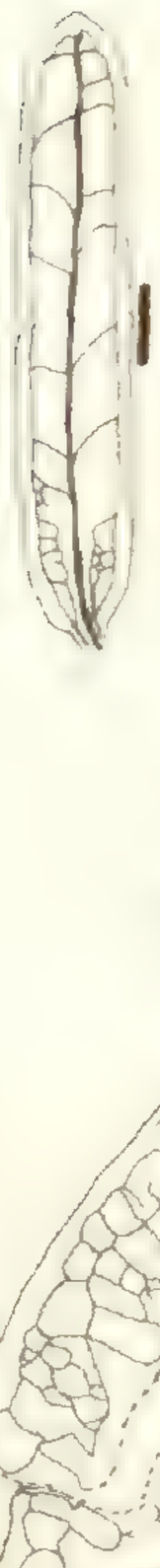
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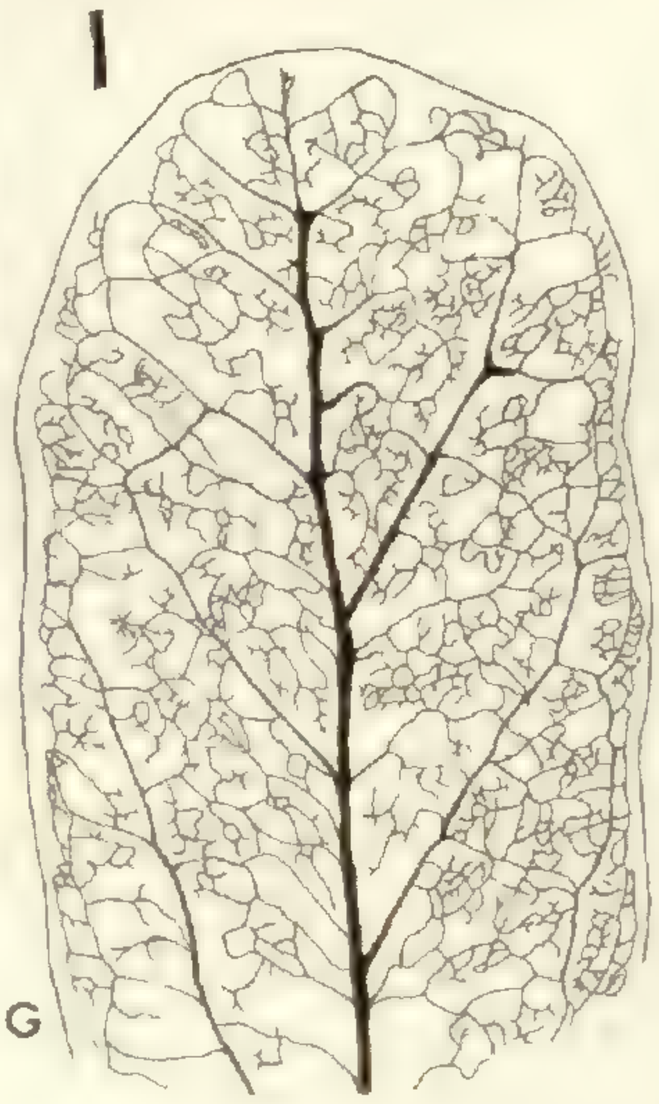
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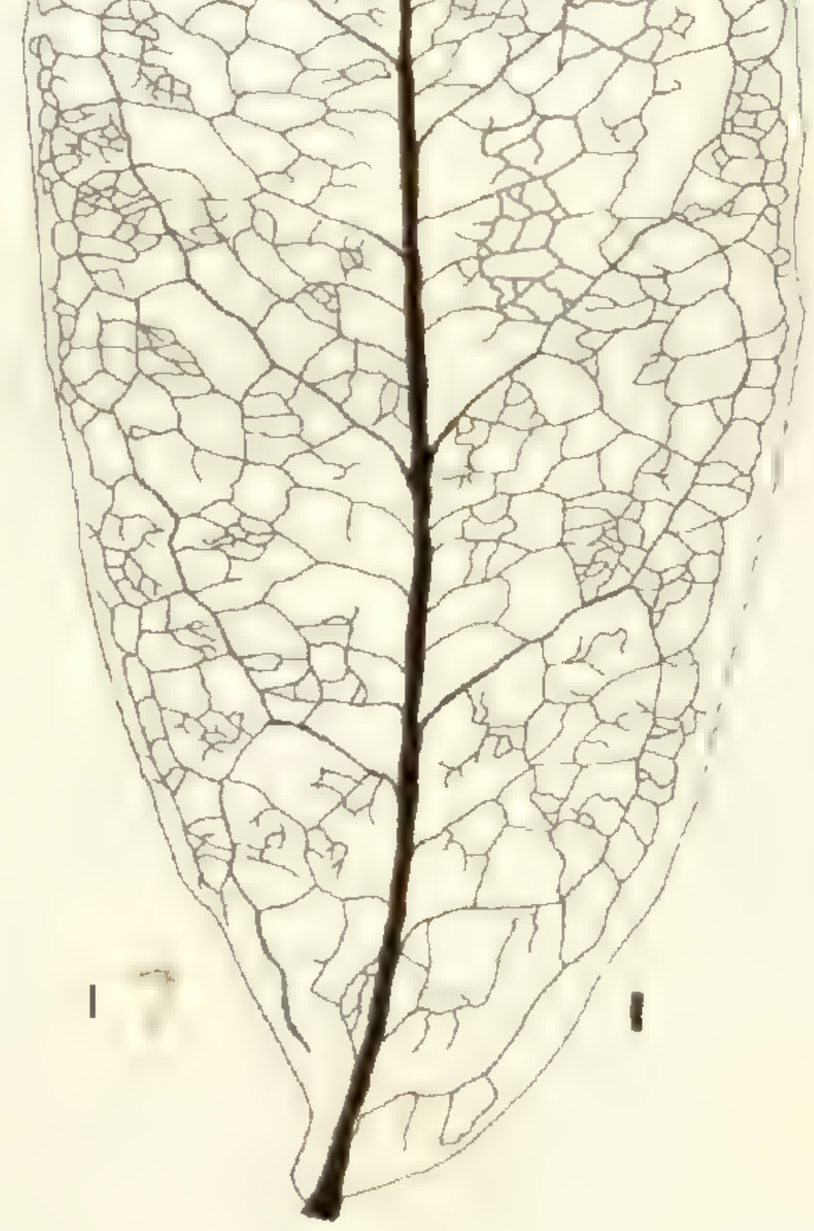
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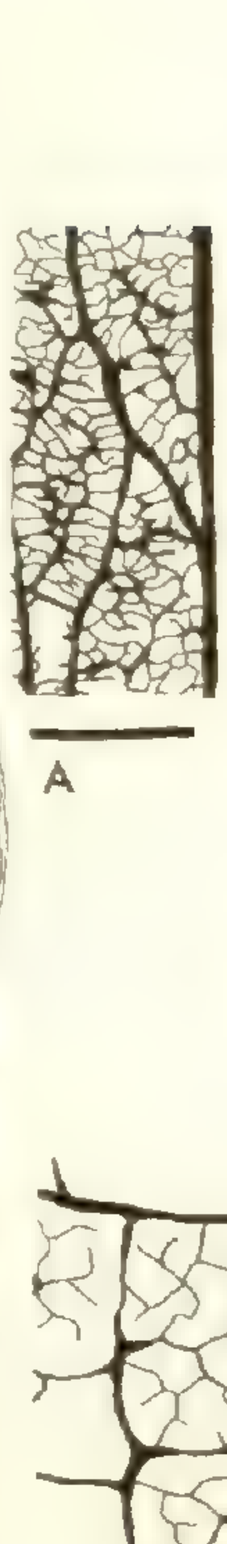

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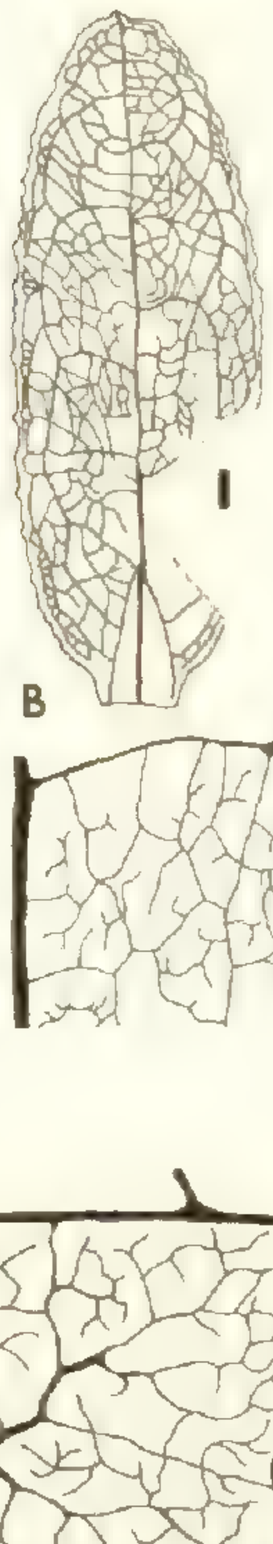

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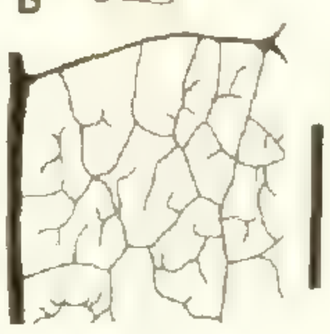

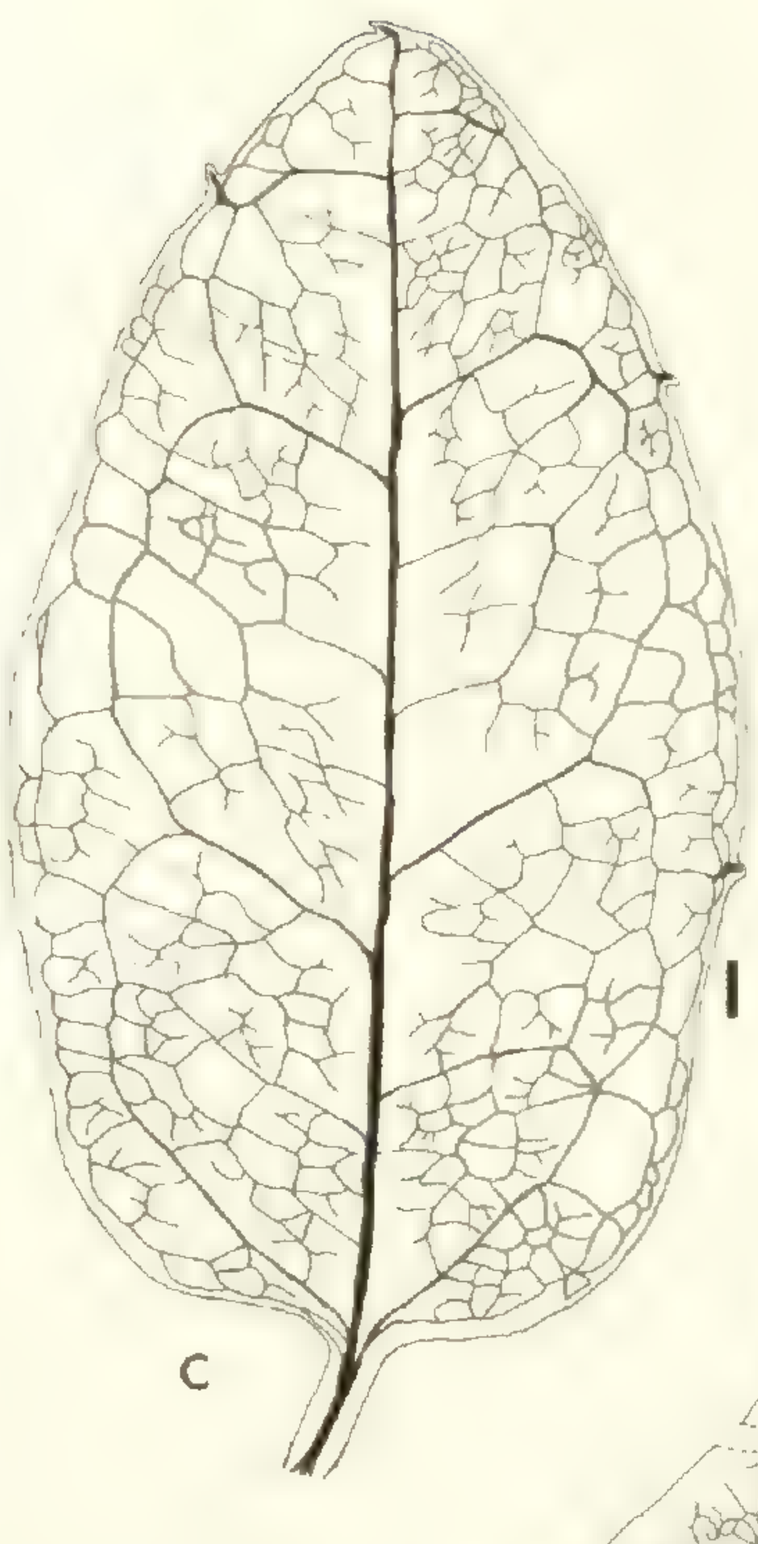

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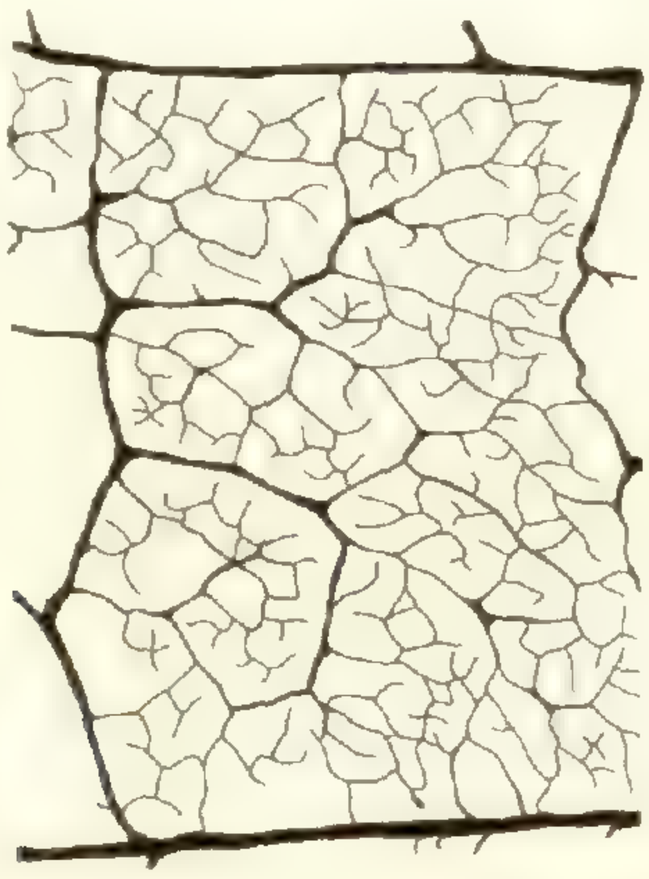

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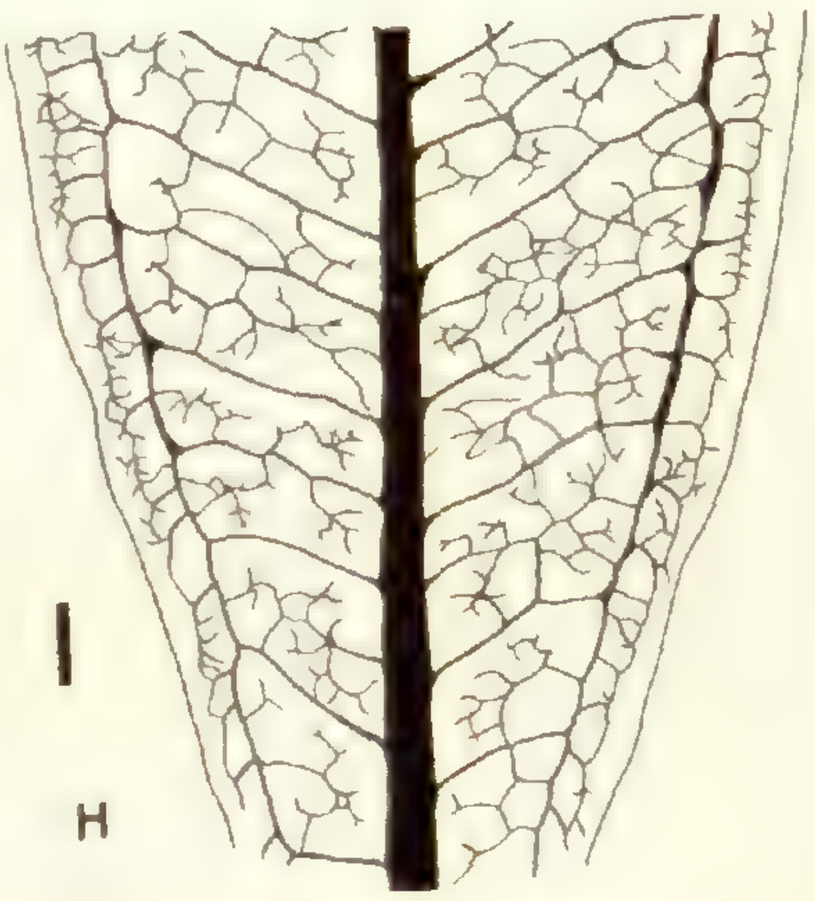
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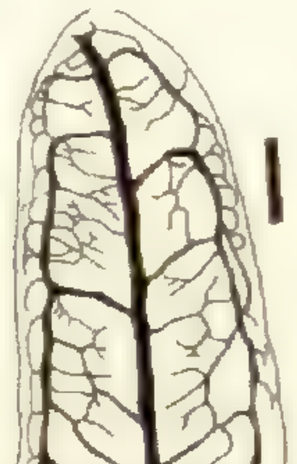
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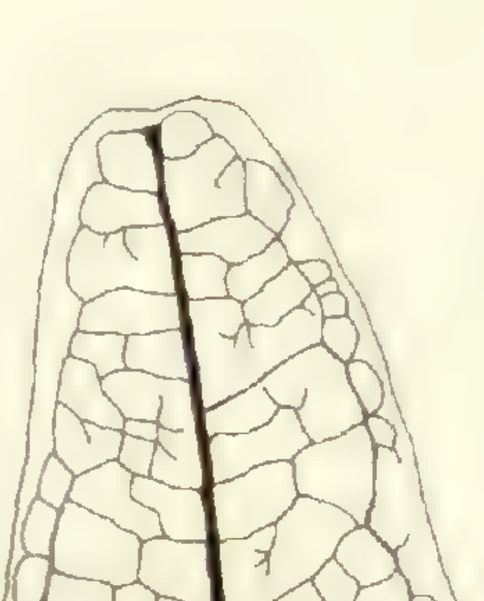
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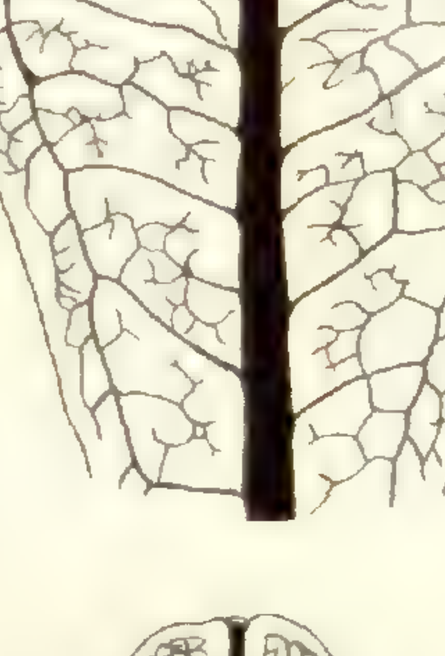
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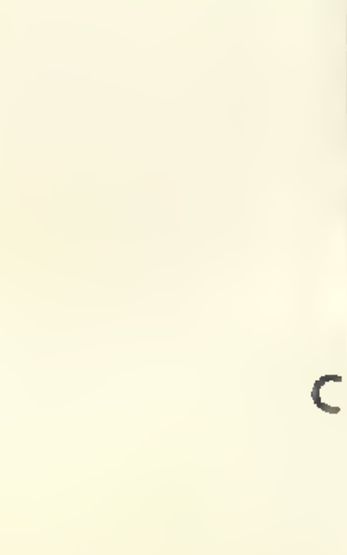
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Rury & Dickison, Leaf Venation Patterns

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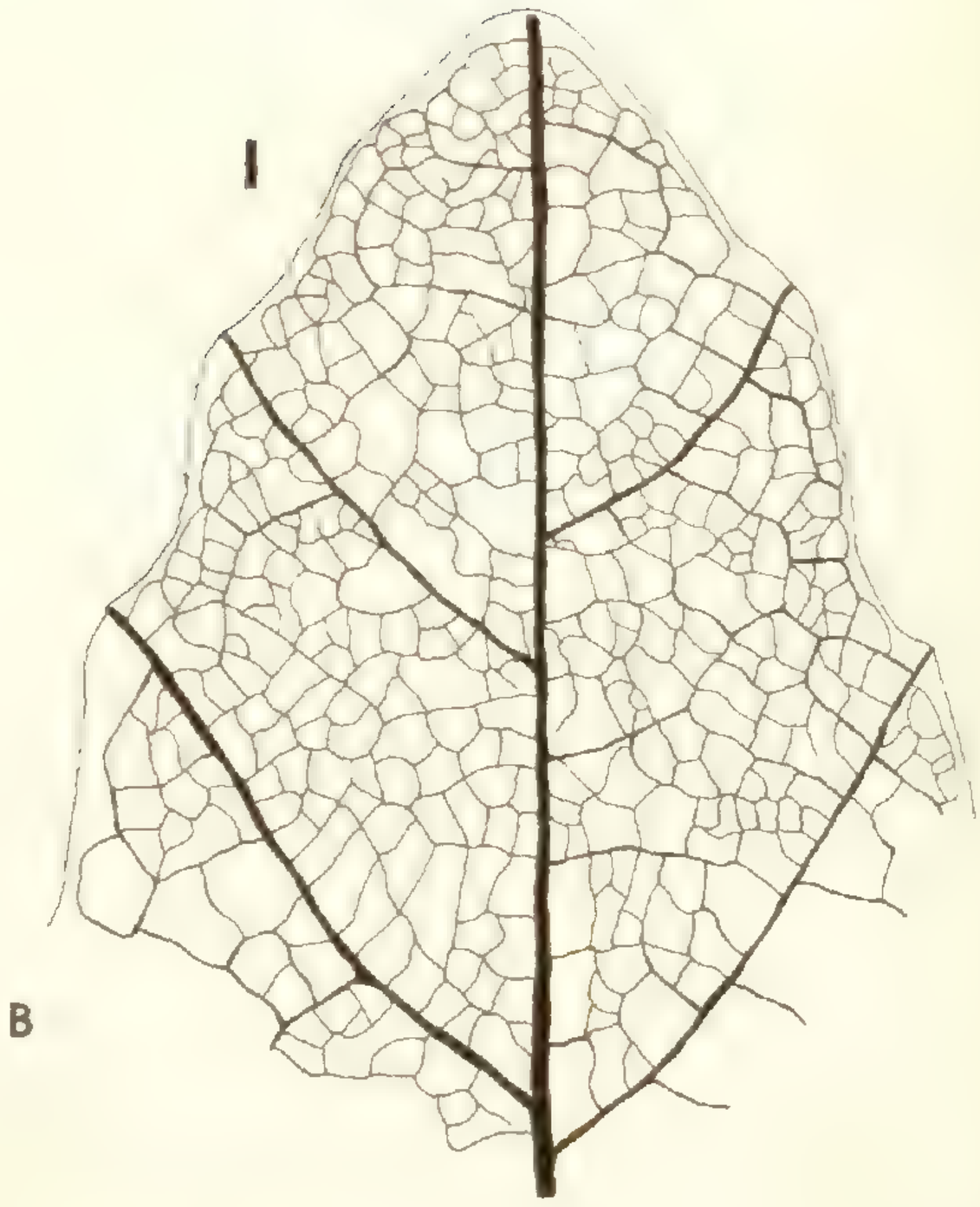

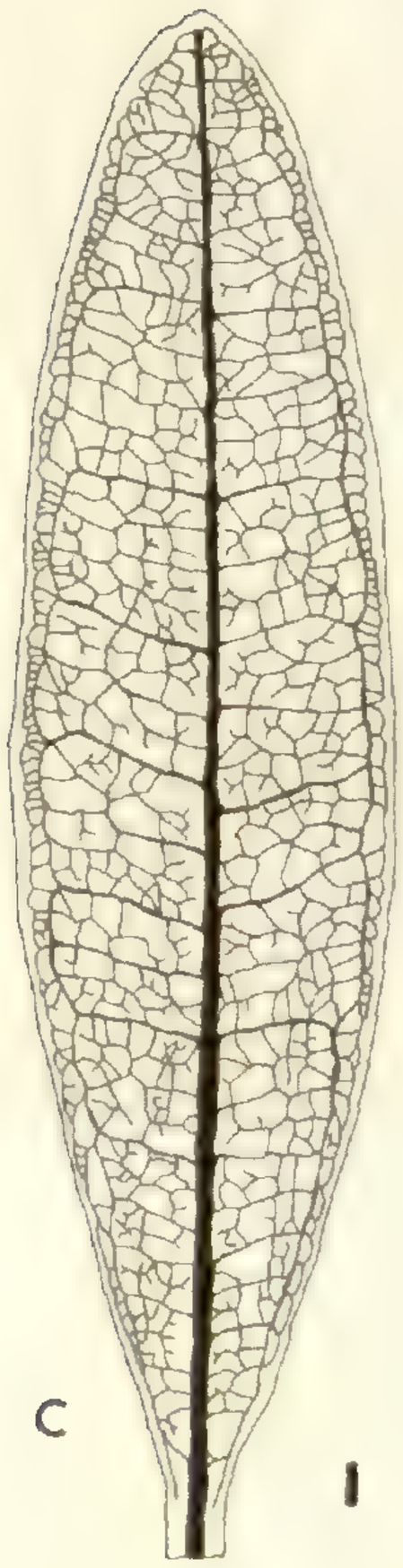

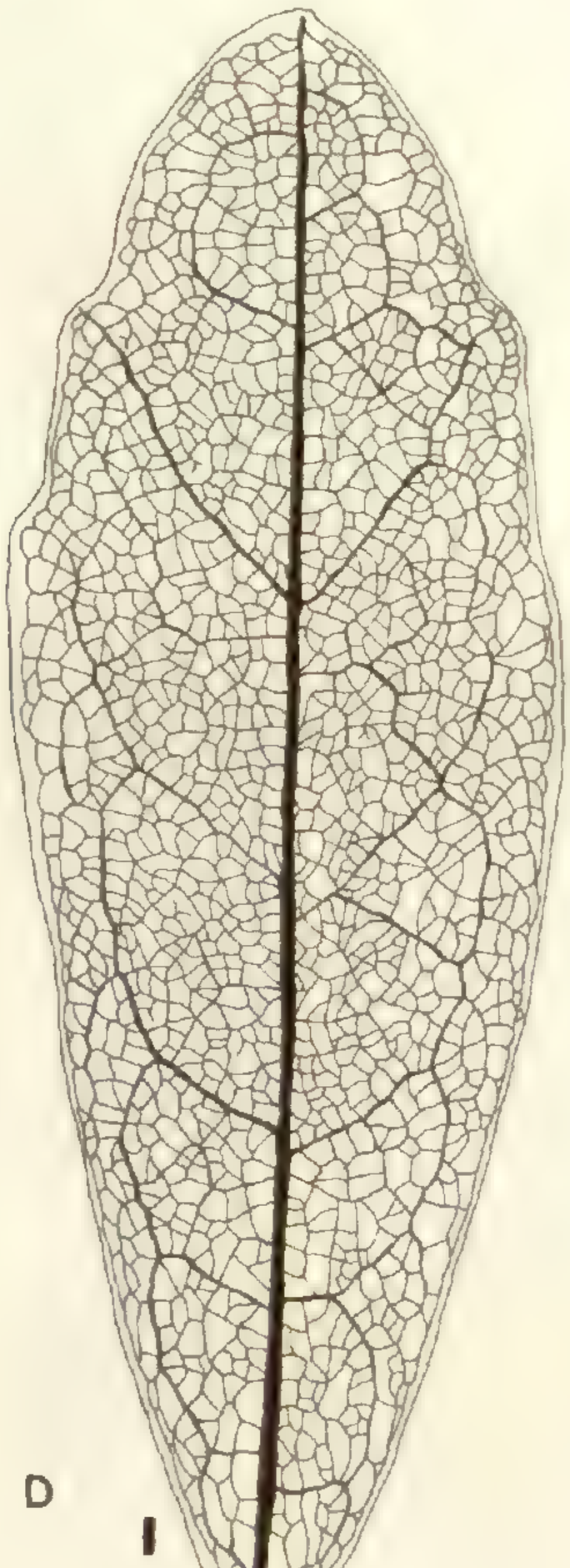

RURY & DICKISON, LEAF VENATION PATTERNS

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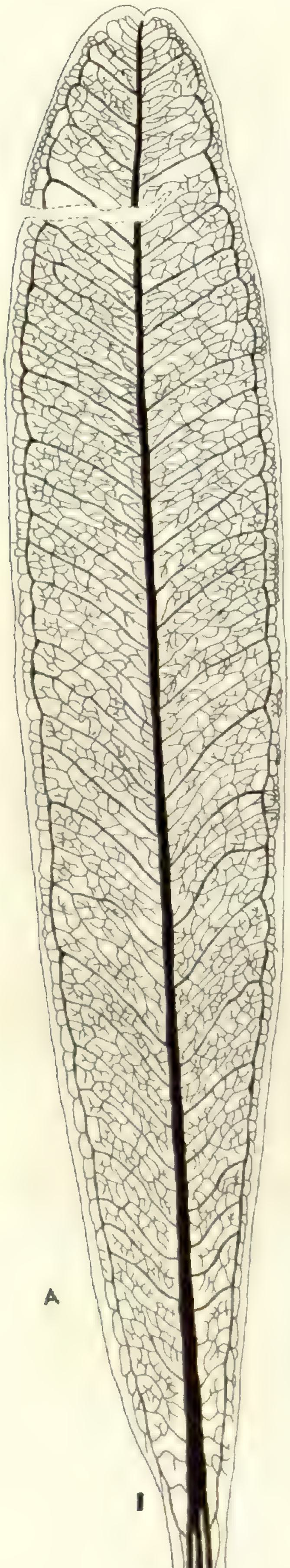

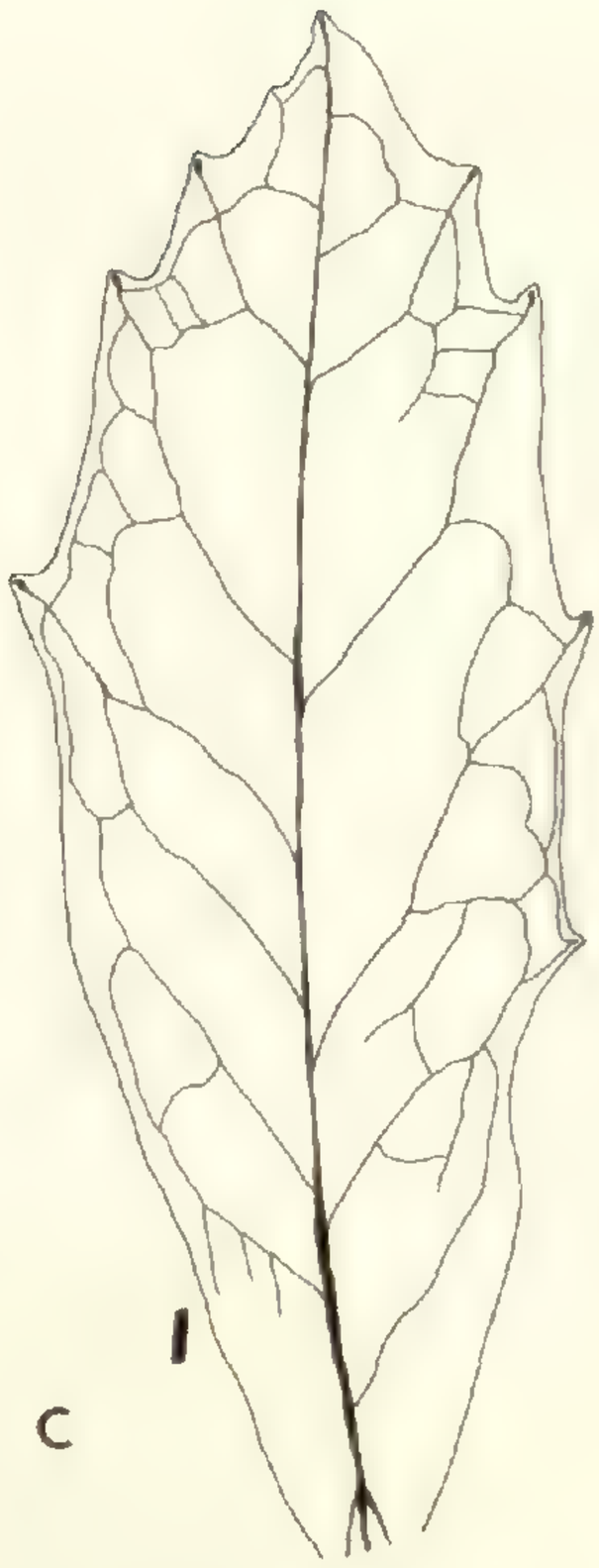

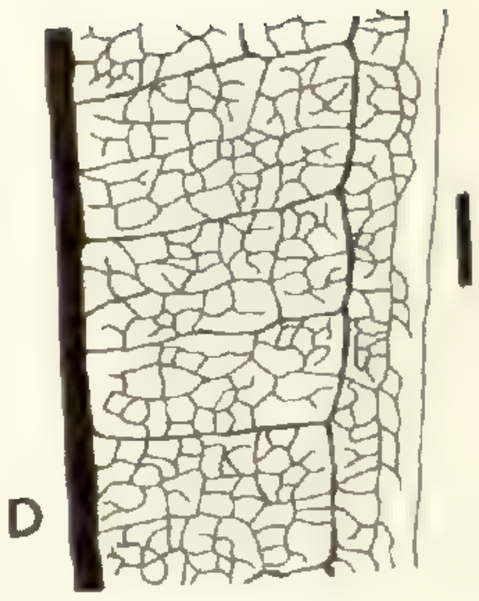

RURY & DICKISON, LEAF VENATION PATTERNS

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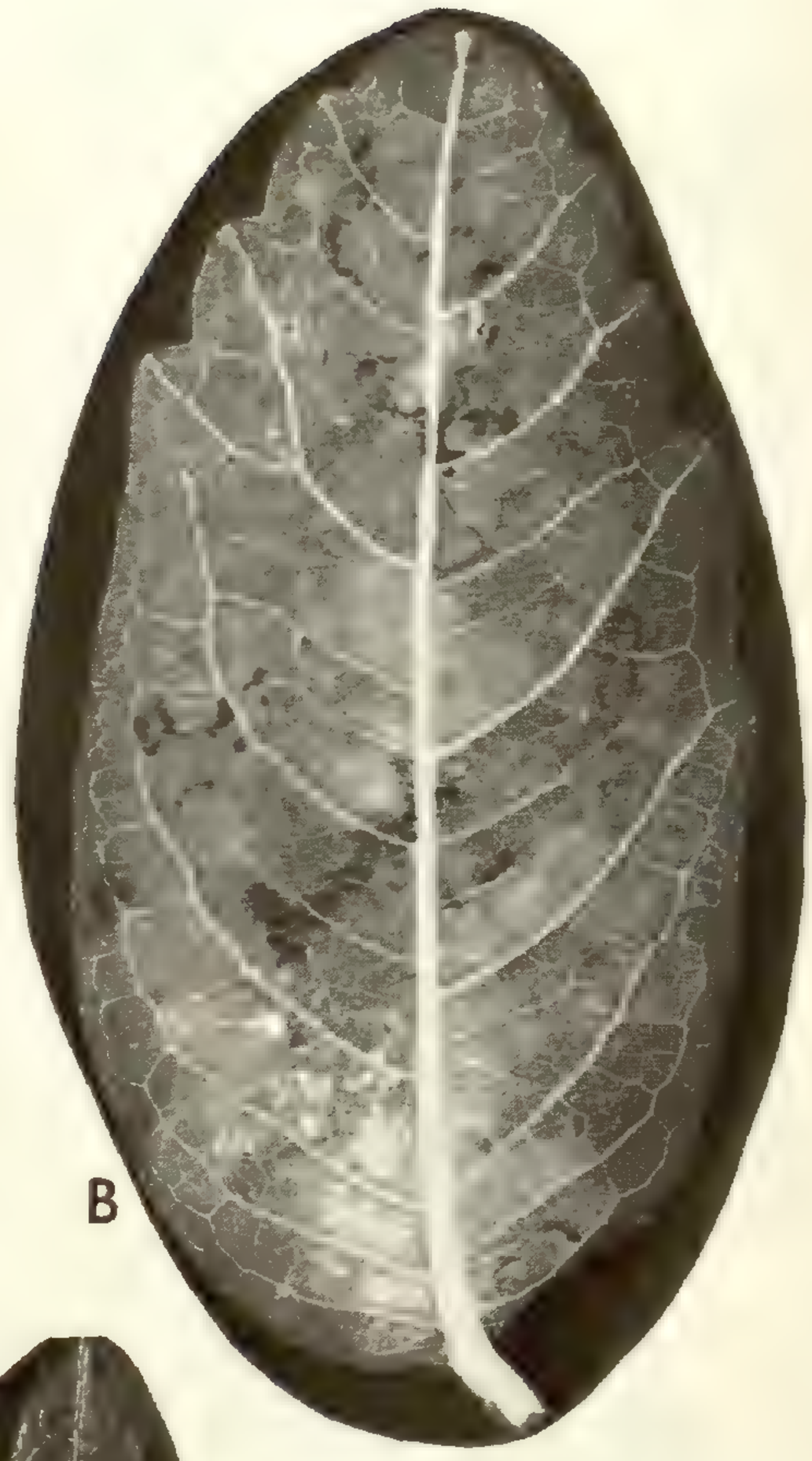
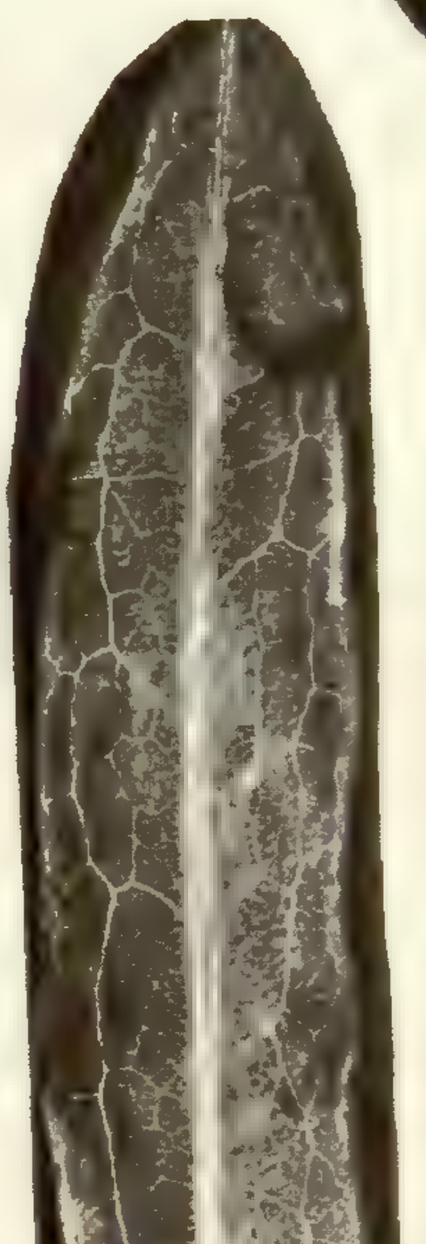
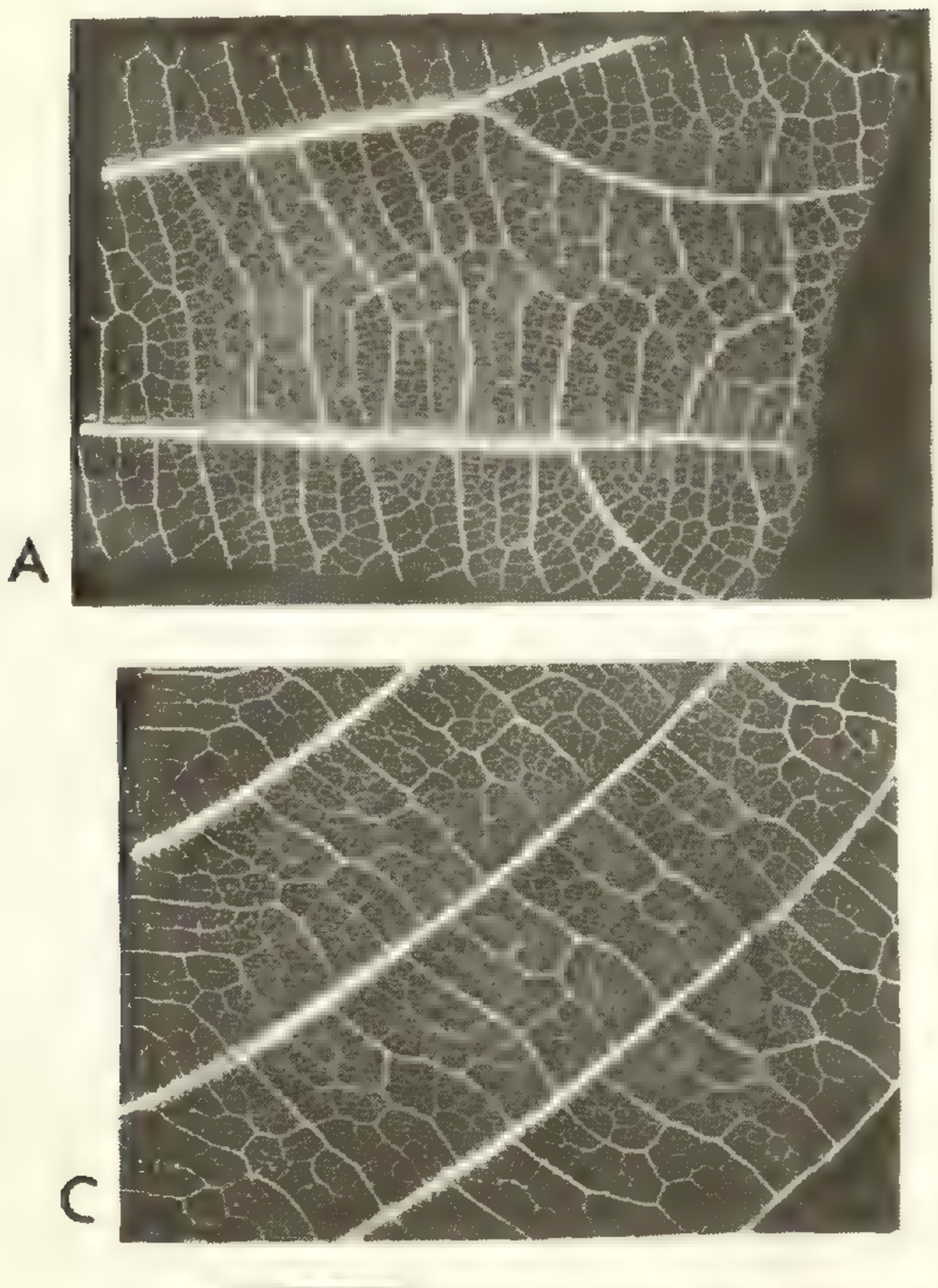
RURY & DICKISON, LEAF VENATION PATTERNS





RURY & DICKISON, LEAF VENATION PATTERNS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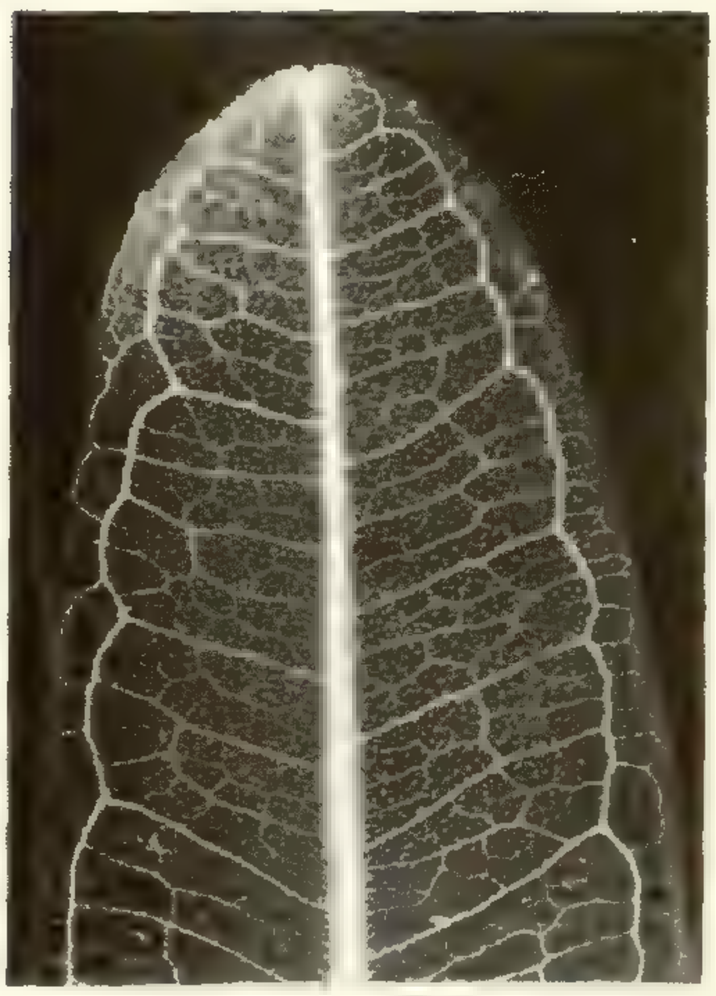
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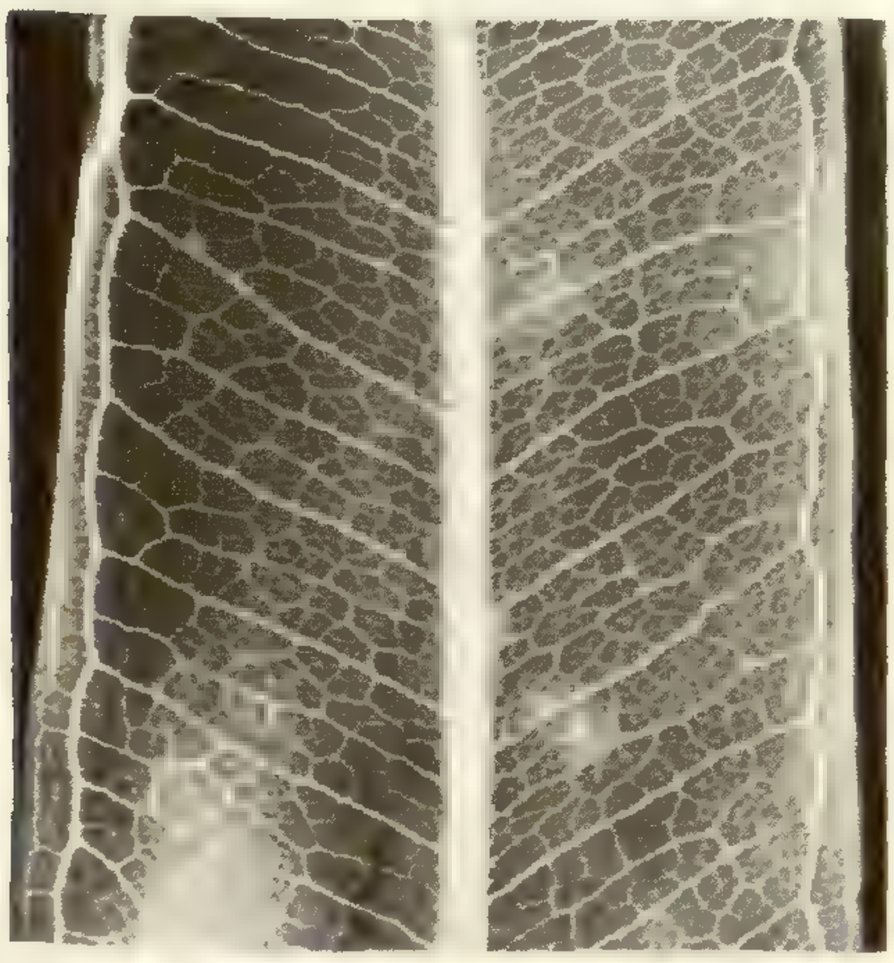
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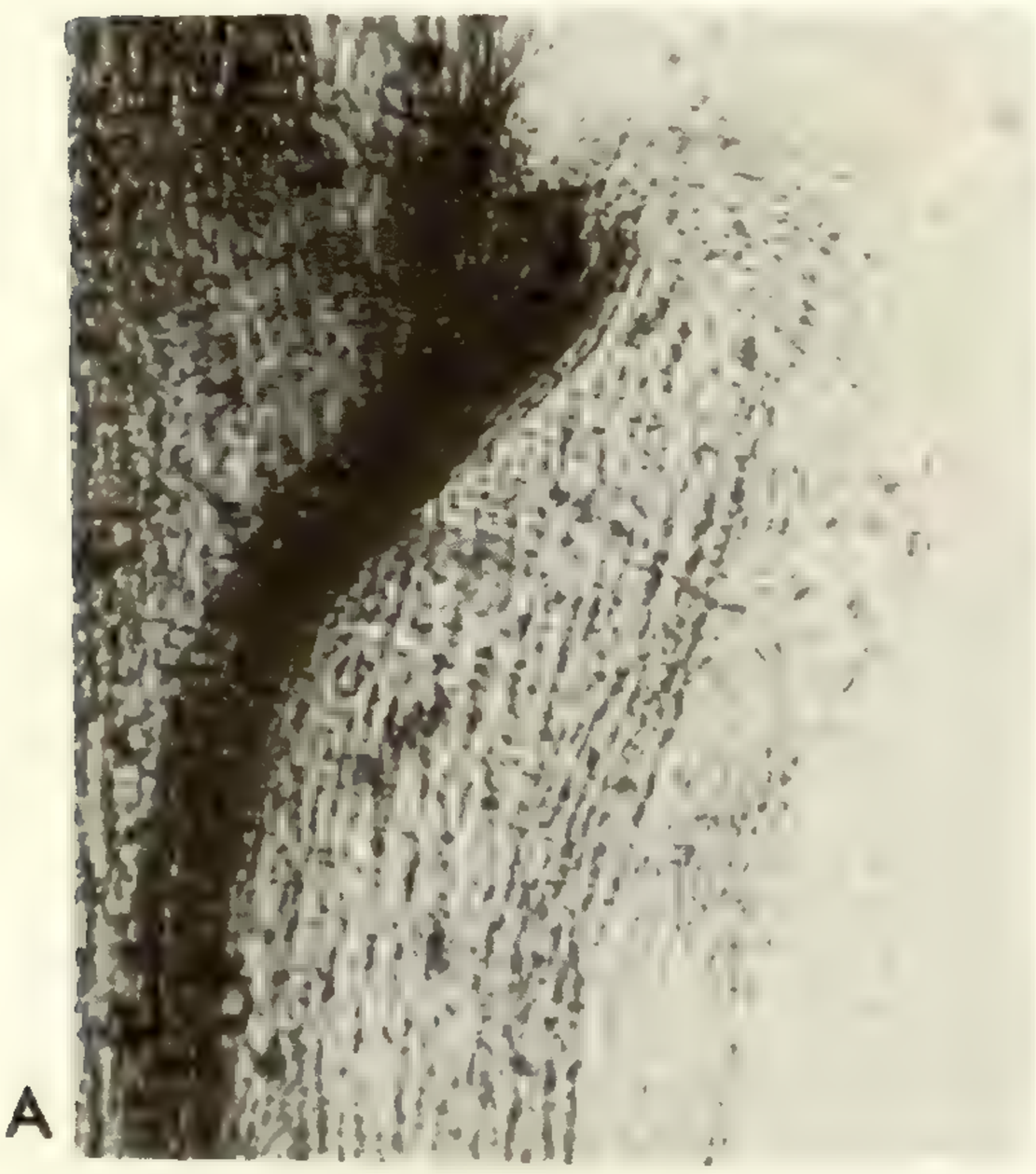
RURY & DICKISON, LEAF VENATION PATTERNS



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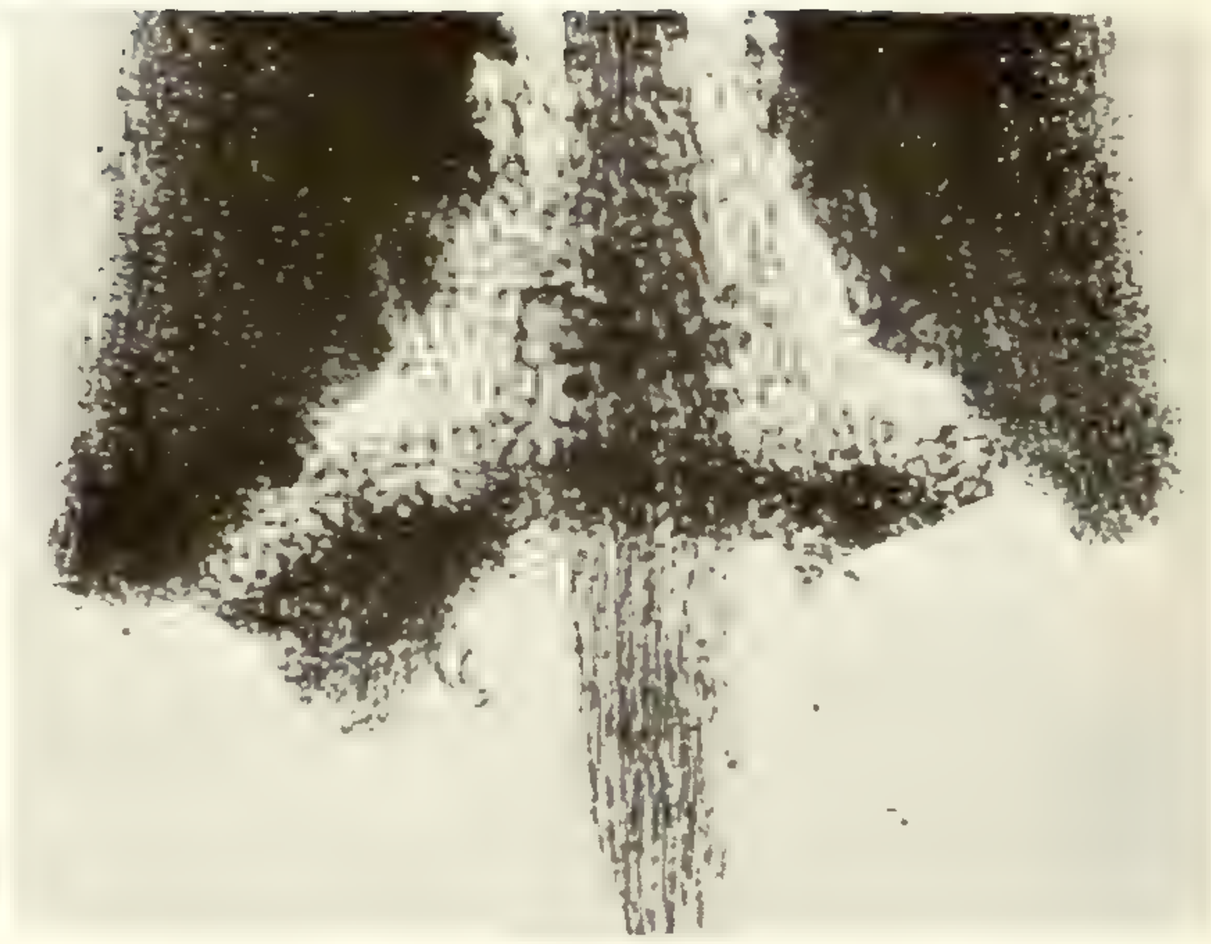

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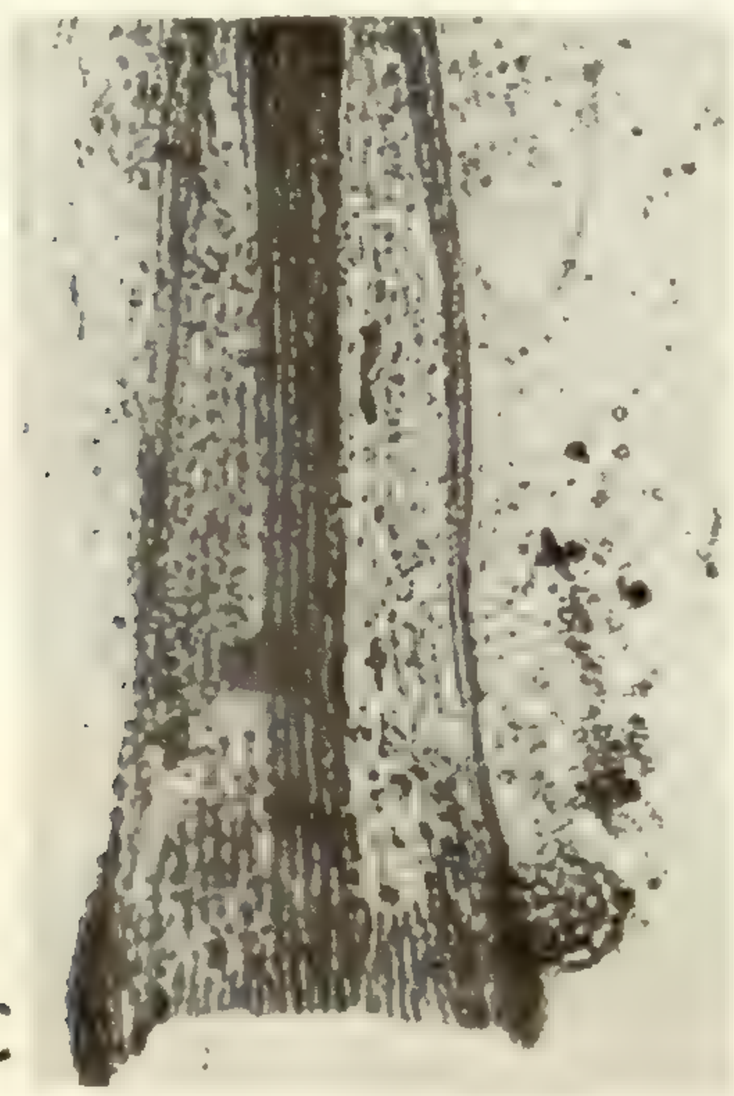

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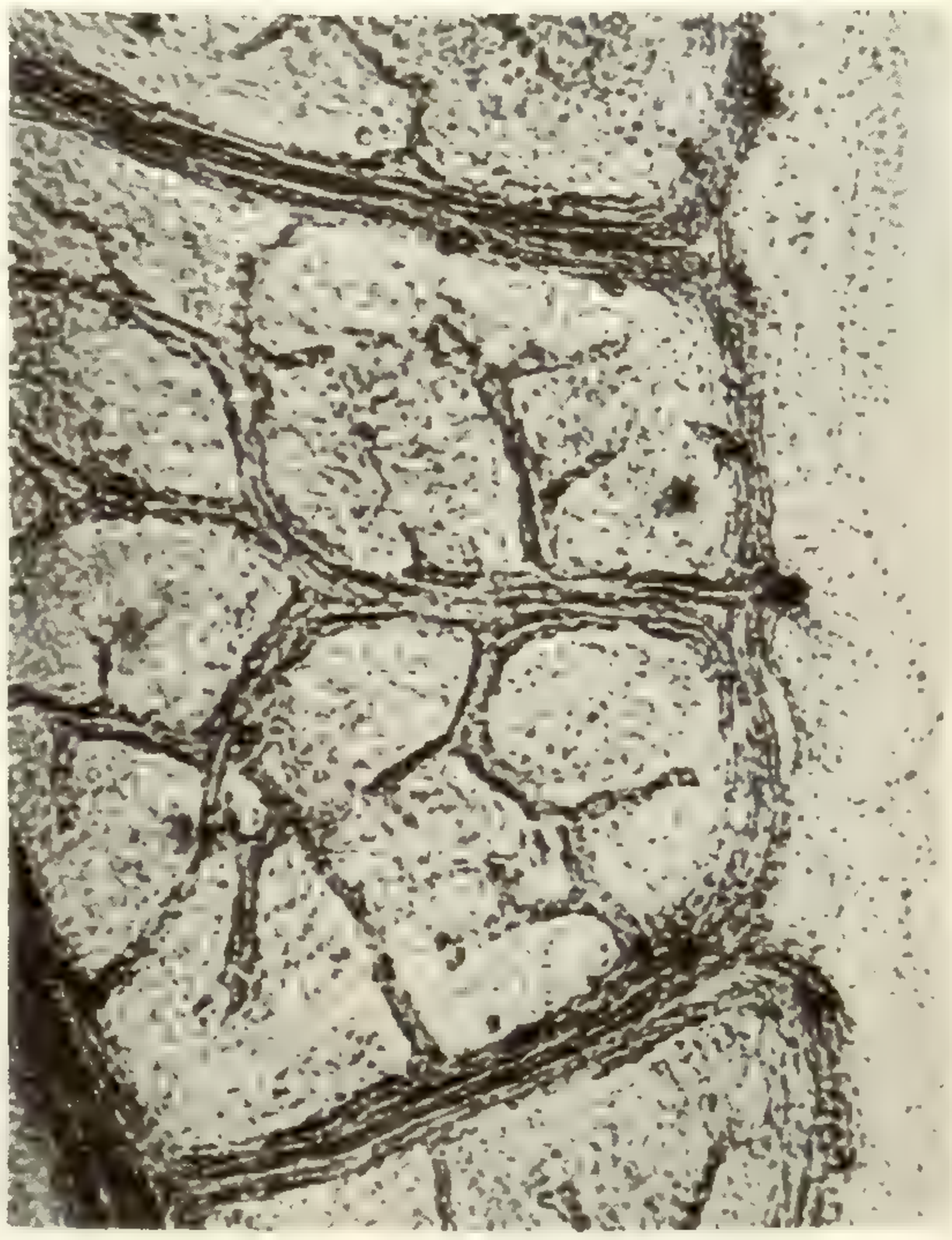

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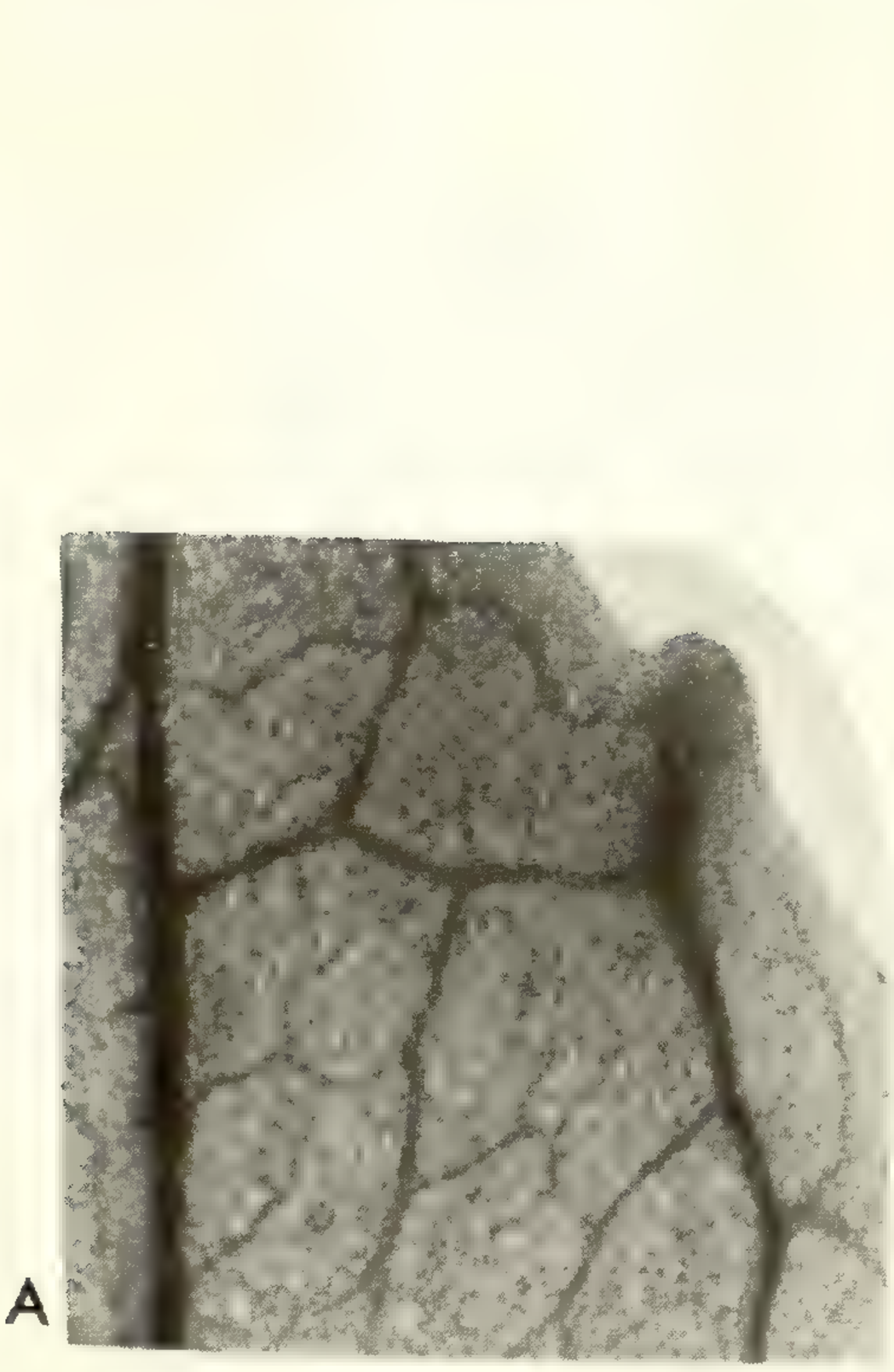
RURY & DICKISON, LEAF VENATION PATTERNS



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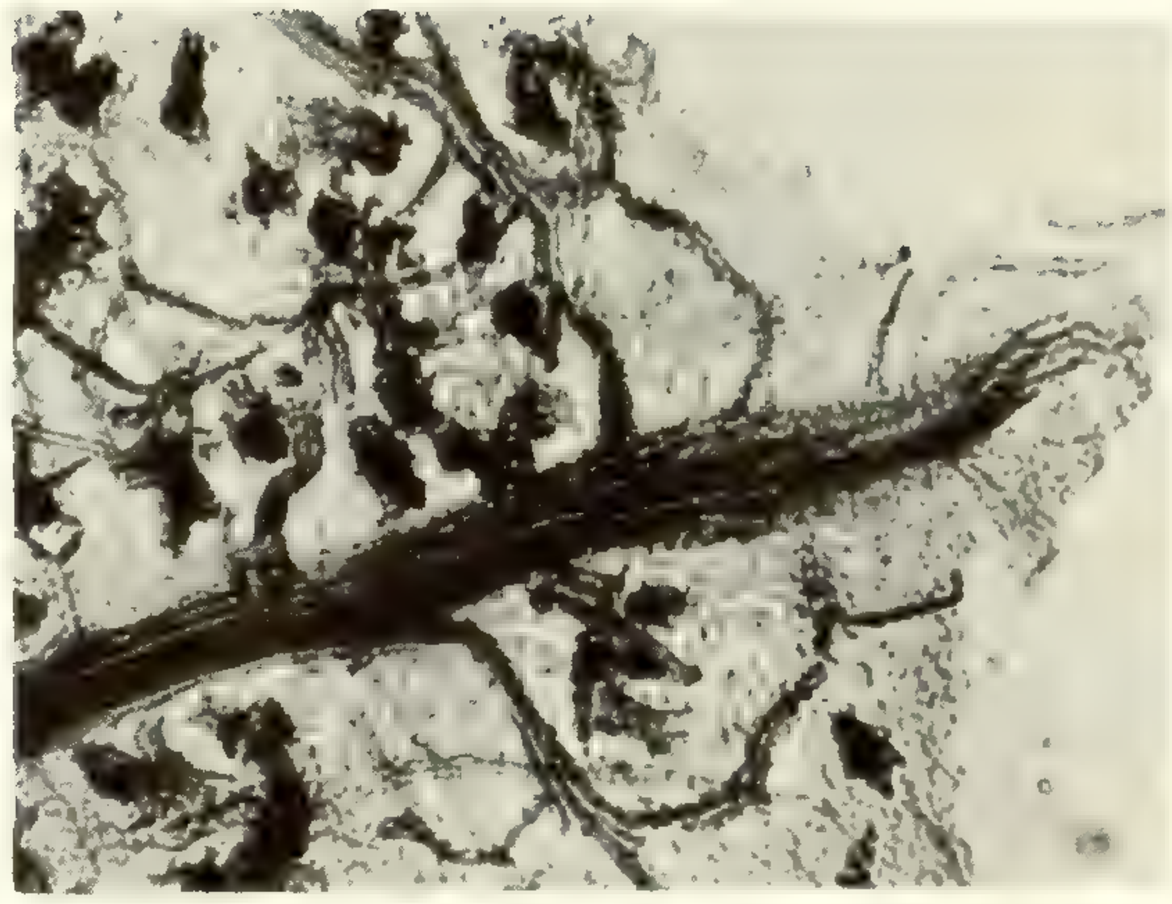

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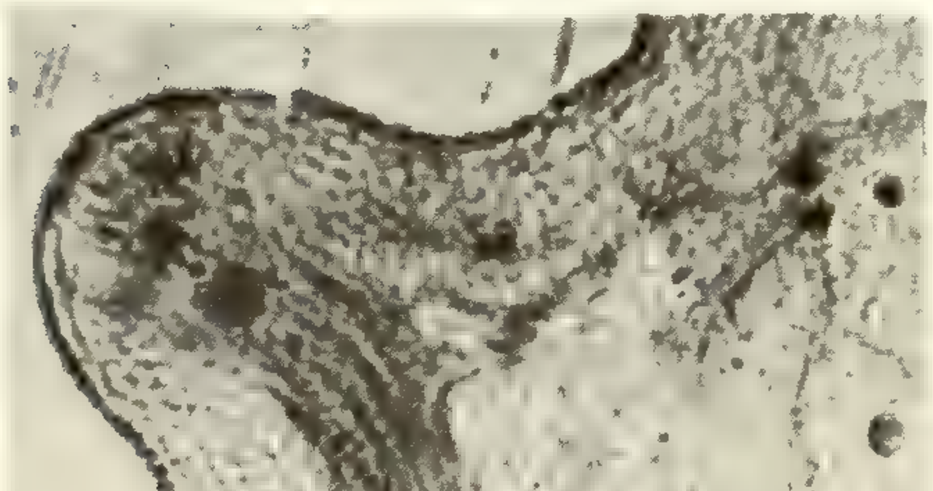

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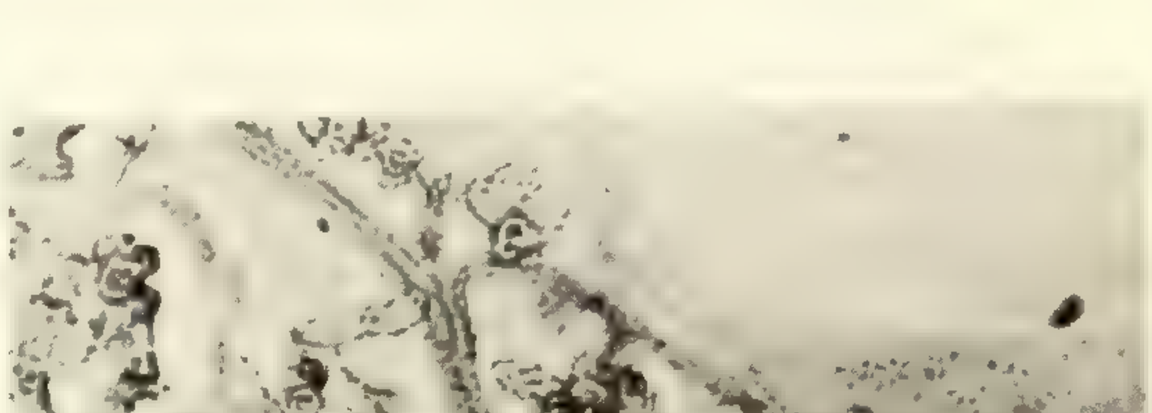

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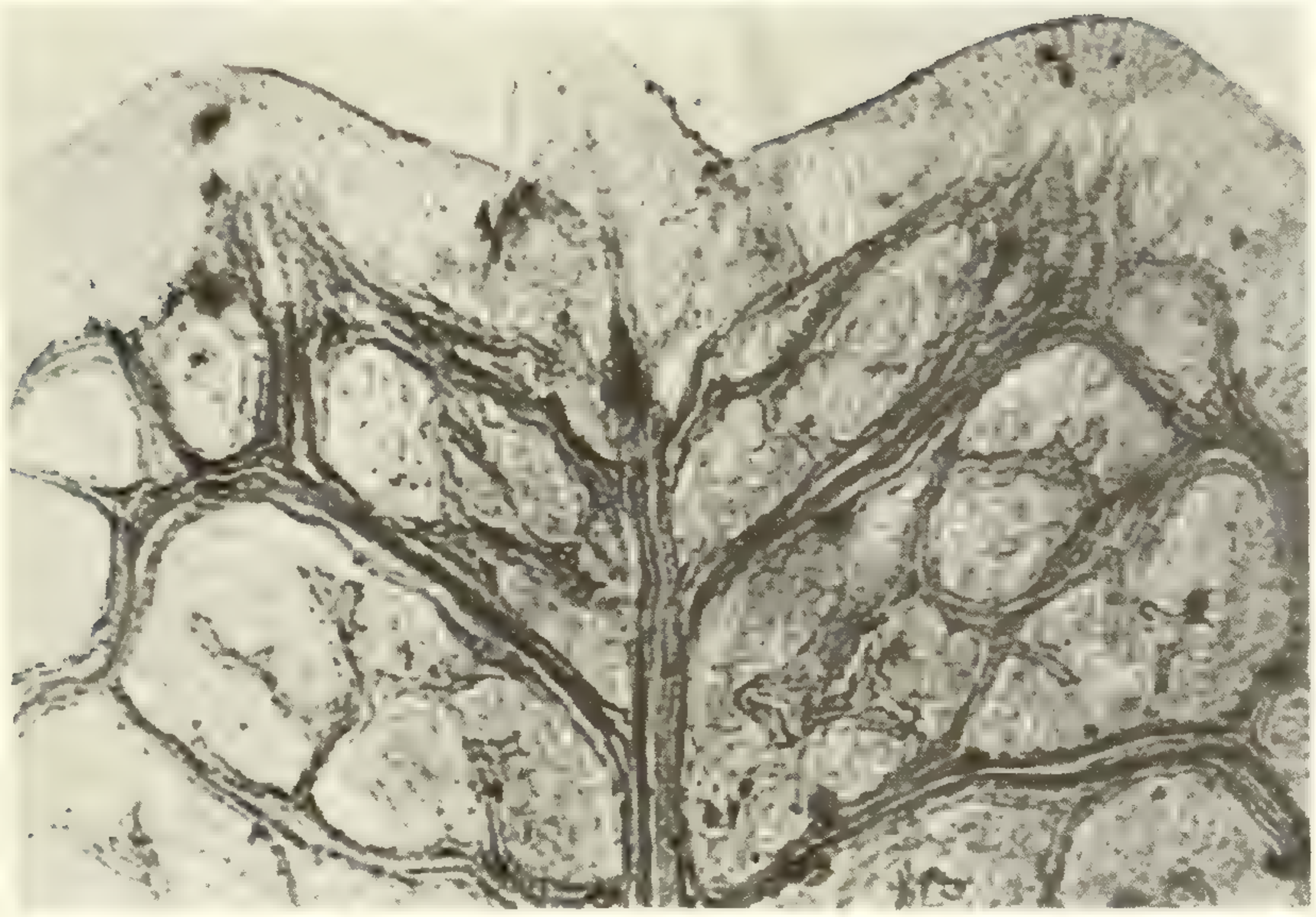

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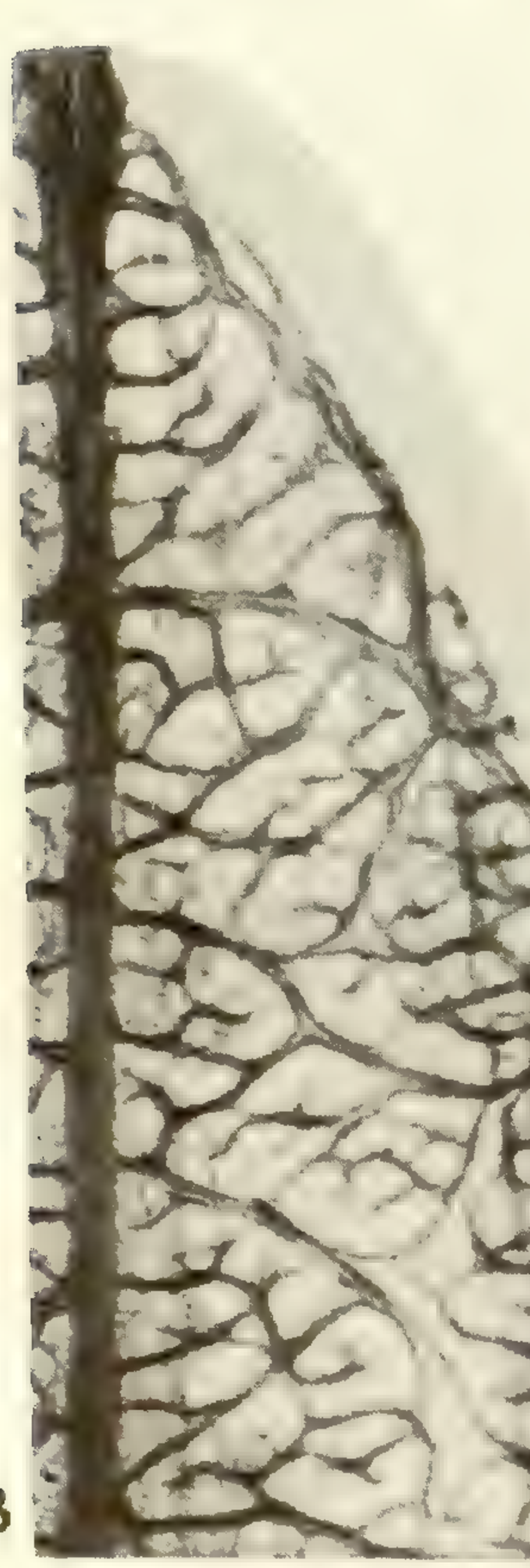

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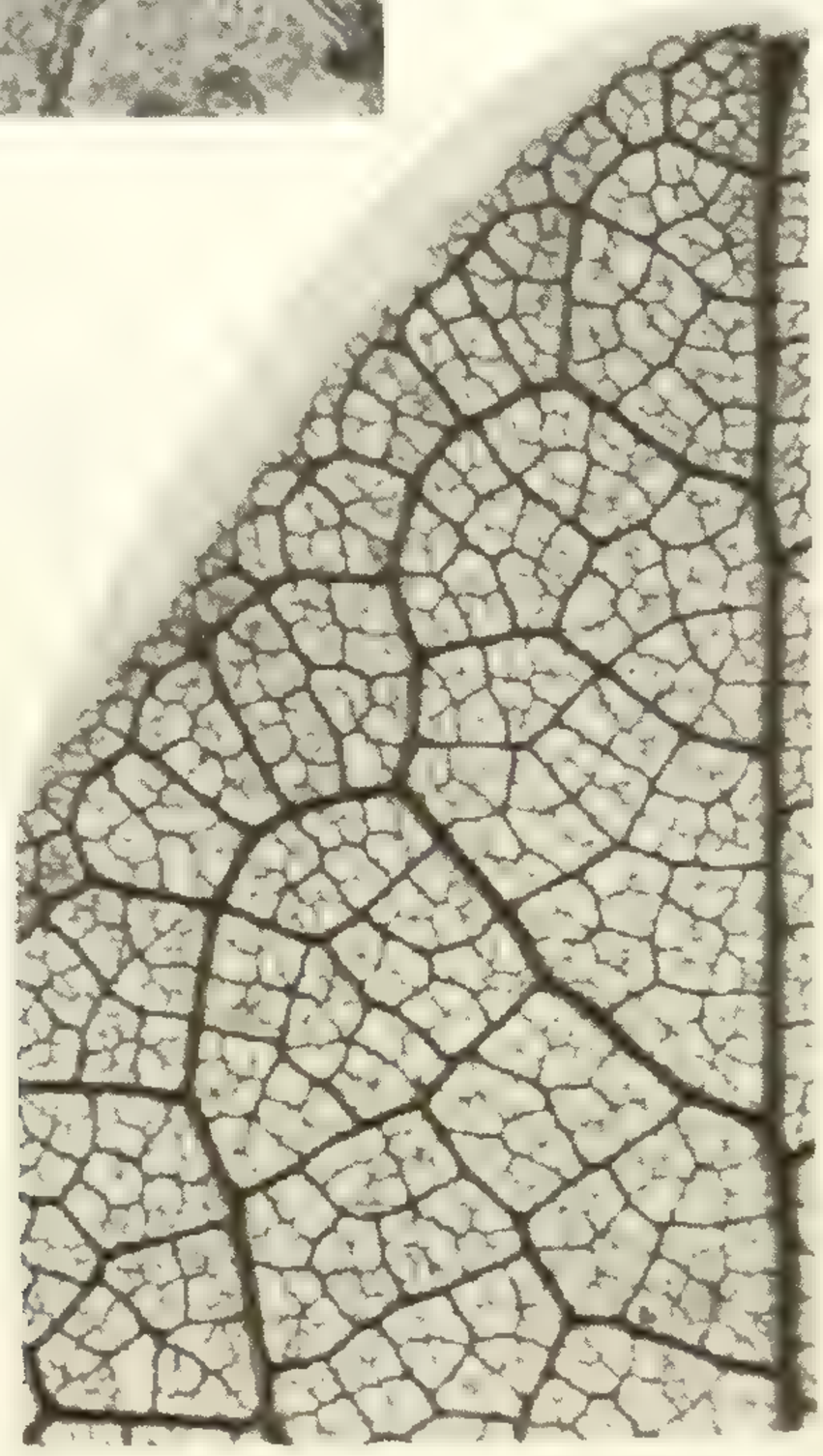

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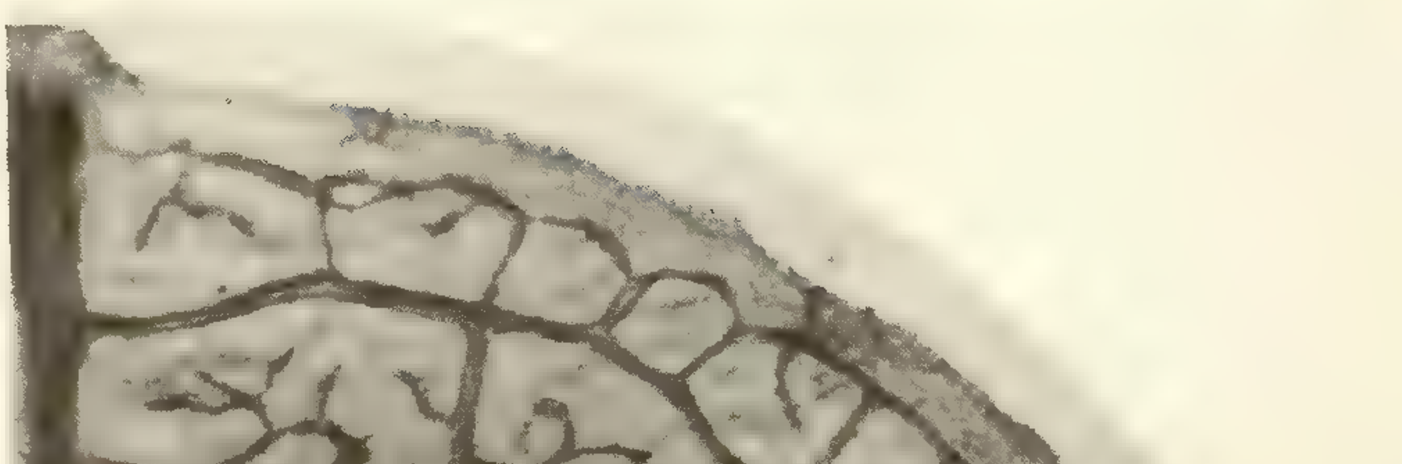

D

RURY & DICKISON, LEAF VENATION PATTERNS

COMPARATIVE ANATOMY AND SYSTEMATICS OF PICRODENDRON, GENUS INCERTAE SEDIS *

W. JOHN HAYDEN

A GENUS OF SMALL dicotyledonous trees which occurs on some of the Bahama Islands and Greater Antilles, *Picrodendron* Planchon has been poorly understood for most of its long history. Before it was recognized as a distinct genus, *Picrodendron* had been confused with three different genera: *Juglans* L., *Rhus* L., and *Schmidelia* L. (= *Allophylus* L.). Moreover, it has been considered as a member of or having affinities with Anacardiaceae (Macfadyen, 1837), Sapindaceae (Richard, 1845), Simaroubaceae (Planchon, 1846; Bentham & Hooker, 1862; Urban, 1920; Moscoso, 1943), Juglandaceae (Grisebach, 1859), Burseraceae (Grisebach, 1866), Terebinthaceae (Hallier, 1908), Picrodendraceae (Small, 1917; and numerous recent authors), Euphorbiaceae (Fawcett & Rendle, 1917; Thorne, 1968; Webster, 1975), and Bombacaceae (Hallier, 1923). Picrodendraceae has been variously placed in Juglandales (Cronquist, 1968; Hutchinson, 1973), Rutales (Scholz, 1964; Takhtajan, 1966), and Euphorbiales (Novák, 1961; Takhtajan, 1969).

This study of the vegetative anatomy of *Picrodendron* and some of its putative relatives has been undertaken in order better to understand its natural relationships. Despite the number of anatomical studies in the literature (Jadin, 1901; Solereder, 1908; Boas, 1913; Webber, 1936; Heimsch, 1942; Record & Hess, 1943; Metcalfe & Chalk, 1950), our information on the anatomy of *Picrodendron* is still incomplete; for example, nodal and petiolar anatomy has apparently never been described. Furthermore, with the exception of Record and Hess (1943), who discussed *Picrodendron* in a family by itself, other anatomists have compared *Picrodendron* only with members of Simaroubaceae, although sometimes doubting that its anatomical similarities with the subfamily Irvingioideae reflected a natural relationship (Boas, 1913; Webber, 1936; Heimsch, 1942). In this paper, the anatomy of *Picrodendron* is described in detail; it is compared to that of its putative relatives and, for the first time, to that of Euphorbiaceae.

DESCRIPTION AND DISTRIBUTION

Picrodendron Planchon. Deciduous trees or shrubs with shaggy bark. Leaves alternate, long-petiolate, trifoliolate; petiole minutely pubescent; stipules present, very small, setiform, caducous or persistent; leaflets leathery, oblong-elliptic, entire, pinnately veined, subglabrous above, pubescent beneath, petiolulate; petiolules jointed at the base. Flowers unisexual, plants dioecious. Male flowers sessile or on a small pedicel, solitary

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or clustered on simple or sparingly branched spikes arising from the axils of fallen leaves of the previous season's shoots, subtended by (1–)3(–7) unequal, imbricate bracts; perianth lacking; stamens 3–numerous on a hemispherical receptacle, forming a globose head; filaments free, short; anthers ellipsoidal, minutely pubescent above, 2-locular, basifixed, dehiscing by longitudinal slits, extrorse; pollen spinose-verrucate; no vestige of an ovary. Female flowers solitary, on slender pedicels arising from the axils of leaves of the current season; the pedicels finely pubescent; sepals 4(–5), lanceolate, unequal, free, valvate, with small glands at the base, sometimes obscurely toothed or ciliate; petals, staminodes, and disc all lacking; ovary superior, 2-locular, sessile, gradually narrowed into a stout, deeply 2-lobed style; stigmas with revolute margins; ovules 2 in each loculus, pendulous from a hemispherical placenta at the top of the loculi, anatropous; raphe ventral; integuments 2; obturator reddish-brown, one per ovule, arising from the placenta and closely covering the micropyle, withering upon maturation of the seed. Fruit a globose drupe; exocarp thin, fleshy, orange, or yellow to greenish-yellow, containing numerous vesicles filled with bitter juice; endocarp hard, indehiscent, obscurely 4-angled. Seed 1 per fruit by abortion, occupying most of the fruit, globular; cotyledons much corrugated, reflexed; radicle superior; endosperm lacking. (The preceding description has been collated from the following authors: Adams, 1972; Britton & Millspaugh, 1920; Engler, 1931; Fawcett & Rendle, 1917, 1920; Grisebach, 1859; Hutchinson, 1973; Planchon, 1846; Small, 1911, 1917; and Willis, 1973). A chromosome count of $2n = 48$ has been reported by Fritsch (1972).

Descriptions of *Picrodendron* in the above-mentioned works contain some contradictions and/or differences in interpretation. Given the small and often ephemeral nature of the stipules, it is not surprising that some authors (e.g., Grisebach, 1859) described the plants as estipulate. The male inflorescence has been described as "a catkin" or "amentaceous" by authors supporting a relationship to the Juglandales (Grisebach, 1859; Small, 1917; Hutchinson, 1973). Alternatively, male inflorescences have been described as "stalked axillary spikes" (Fawcett & Rendle, 1917) or "strict catkin-like pseudo-racemes or narrow thyrses" (Willis, 1973). Small (1917) suggested that the hemispherical receptacle of the male flowers might be formed by the coherence of the lower parts of the filaments, although most authors describe the filaments as free. Fawcett and Rendle (1917) erroneously reported an inferior ovary for *Picrodendron*, but later corrected this mistake (1920). Pax and Hoffmann (1931) and Engler (1931), citing Fawcett and Rendle's earlier paper, unwittingly continued this error. The ovary is unquestionably superior. Only Fawcett and Rendle (1917, 1920) and Engler (1931) mentioned the ventral raphe, the obturator, and the presence of glands on the sepals of female flowers.

Until recently *Picrodendron* had been divided into three species as summarized by Small (1917):

1) *P. baccatum* (L.) Krug & Urban, from Jamaica, the Cayman Islands, and Swan Islands.

2) *P. macrocarpum* (A. Rich.) Britton, from Cuba and the Bahamas.
3) *P. medium* Small, from Hispaniola.

These species were separated largely on characters of the leaves and fruit. William T. Gillis (1974, and pers. comm.), however, has concluded from field and laboratory studies that, even though these plants vary, they do not do so in any way which would uphold the division of the genus into three species. He has therefore decided (1974) that the genus is monotypic and that the correct name for the single species is *P. baccatum* (L.) Krug & Urban.

The distribution of *Picrodendron* is striking in that it is present in Cuba, Jamaica, and Hispaniola, but is absent from Puerto Rico, a distribution shared by 20 other genera in the Greater Antilles (Howard, 1973). *Picrodendron* inhabits arid, rocky (usually limestone) areas, maritime rocks, margins of saline water in deltas, or the landward margins of mangrove formations.

MATERIALS AND METHODS

Specimens used in this investigation and their documentation are listed in TABLE 1. For the most part, standard techniques were used in tissue preparation and sectioning, and are described in detail elsewhere (Hayden, 1976).

Diagnostic characters used to describe leaves were selected from Esau (1965) and Fahn (1974), among other sources. Terminology used in characterizing leaf architecture follows that proposed by Hickey (1973). Characters and terminology employed in describing wood were selected from Tamolang *et al.* (1963) and Tippo (1941), and are essentially in accord with those recommended by the Committee on Nomenclature, International Association of Wood Anatomists, *International Glossary of Terms Used in Wood Anatomy* (1957).

ANATOMICAL DESCRIPTION

Picrodendron baccatum

INTERNODE. Epidermis of the young axis was not observed; in the specimen examined (*Gillis 10975*) it had already been replaced by a periderm of superficial origin. Scattered among the parenchyma cells of the cortex are idioblasts containing either an amber-colored substance,[1] mucilage, druses, or prismatic crystals. Some of the phloem parenchyma cells contain druses, prismatic crystals, or an amber-colored substance. Groups of thick-walled fibers occur external to the conducting cells of the phloem, forming an incomplete ring around this tissue. Xylem, at least after some secondary growth has occurred, is in the form of a complete ring. Imperforate tracheary elements are thick walled, and pores are either solitary or in short radial multiples. Tangential diameters of pores range

[1] This substance turns dark gray or black in 4 percent iron alum.

TABLE 1. Specimens examined.[a]

SPECIES	COLLECTOR	LOCALITY [b]	TYPE OF SPECIMEN [c]	XYLARIUM [d]	HERBARIUM VOUCHER [e]
Picrodendron baccatum (L.) Krug & Urban	*Gillis 10893*	Florida	w* l* t*	—	FTG
Picrodendron macrocarpum (A. Rich.) Britton	*Gillis 10975*	Florida	w* l* t*	—	FTG
	Gillis 6963	Florida	w* l* t*	—	FTG
Picrodendron medium Small	*Stadtmiller 171*	Haiti	w	SJRW 19616	—
Juglans major (Torrey) Heller var. **glabrata** Manning	*Frejnik s.n.*	Mexico	w (slide only)	USW[f] 19742	—
Desbordesia sp.	commercial sample	Gaboon	w	SJRW 12804	—
Irvingia gabonensis (Aubrey-Lecomte) Baillon	commercial sample	Gaboon	w	SJRW 12841	—
Irvingia malayana Oliver ex Benn.	—	—	w (slide only)	USW[g]	—
Klainedoxa buesgenii Engler	*C. Donis 405*	Congo	w	USW 24403	BR
Klainedoxa gabonensis Pierre ex Engler	—	Belgian Congo	w	USW 18322	BR
	—	—	w (slide only)	USW[h]	—
Oldfieldia africana Bentham & Hooker f.	commercial sample	Sierra Leone	w	USW 19900	—
Celaenodendron mexicanum Standley	*Ortega 35*	Mexico	w	USW 3886	—
Piranhea longepedunculata Jablonski	*Breteler 5096*	Venezuela	w	USW 35682	MER, NY, U, US, WAG
Piranhea trifoliata Baillon	*Capucho 493*	Brazil	w	USW 22377	IAN
	A. Ducke s.n.	Brazil	w	USW 31485	MAD
	—	—	w (slide only)	USW[i]	—

[a] Additional information concerning the *Picrodendron* specimens is contained in APPENDIX 1.
[b] Political units are stated as originally shown.
[c] w = wood, l = leaf, t = twig; an asterisk (*) indicates a fluid-preserved specimen.
[d] Xylarium abbreviations follow Stern (1967).
[e] Herbarium abbreviations follow Holmgren and Keuken (1974).
[f] Originally received at USW from Archie F. Wilson Collection (907) as *Juglans pyriformis*.
[g] Received at USW from KEPW.
[h] Received at USW from PFPW.
[i] Received at USW from MERW.

from 17 to 38 μm. Vascular rays appear to be either uni- or biseriate. Pith cells are roughly circular in cross section and have sclerified walls. Prominent intercellular spaces are present in the pith. Some pith cells have evident cytoplasm while others are filled with an amber-colored substance which renders other cytoplasmic contents difficult to detect. Neither crystals nor secretory cavities were observed in the pith.

Bark of twigs in their second season of growth consists of periderm, cortex, primary phloem, and secondary phloem; cells with amber-colored deposits are frequent throughout these four tissues. Groups of thick-walled fibers are scattered here and there in the secondary phloem. Each group of fibers is surrounded by strands of sclerified crystalliferous cells which are in turn surrounded by cells containing amber-colored deposits. The extraxylary fibers formed during primary growth are thus easily distinguished from those formed during secondary growth since only the latter are surrounded by crystalliferous cells. Neither secretory canals nor cavities were observed in the bark at any stage of development.

NODE AND PETIOLE. The node is characterized by three leaf traces, each of which departs from a separate gap in the stele as it enters the petiole. Serial sections from an internode to the super-adjacent node reveal that the median trace is first to separate from the stele, at about 3.5 mm. below the insertion of the petiole. Two lateral traces become separate from the stele at approximately 2.5 mm. below the node. At this level the traces are embedded in cells of the cortex. External to each trace there are a few groups of thick-walled fibers.

At the level in which the leaf traces pass into the petiole, several changes become apparent. First, leaf traces are embedded in a groundmass of small, tightly packed parenchyma cells which mark the position of the future leaf abscission zone; these cells are distinguished from cells of the normal stem cortex by their smaller size and the absence of idioblasts. Second, the three gaps in the stele are nearly closed. Finally, groups of fibers external to the leaf traces are no longer present but are situated between the leaf traces and the stele.

At the proximal end of the petiole, the three leaf traces are arranged in the form of a broad V. Although no extraxylary fibers are associated with the traces at first, they reappear at higher levels. Progressing up the petiole, one observes the following changes within approximately the first 5 mm.: first, the lateral traces break up, each forming two or three traces of unequal size; then, some of the smaller traces become inverted and displaced to a position between the tips of the V; finally, all of the traces expand somewhat and form a more or less continuous but irregularly shaped ring of vascular tissue. The configuration attained at this level remains essentially unchanged throughout the petiole except at the extreme distal end (see below).

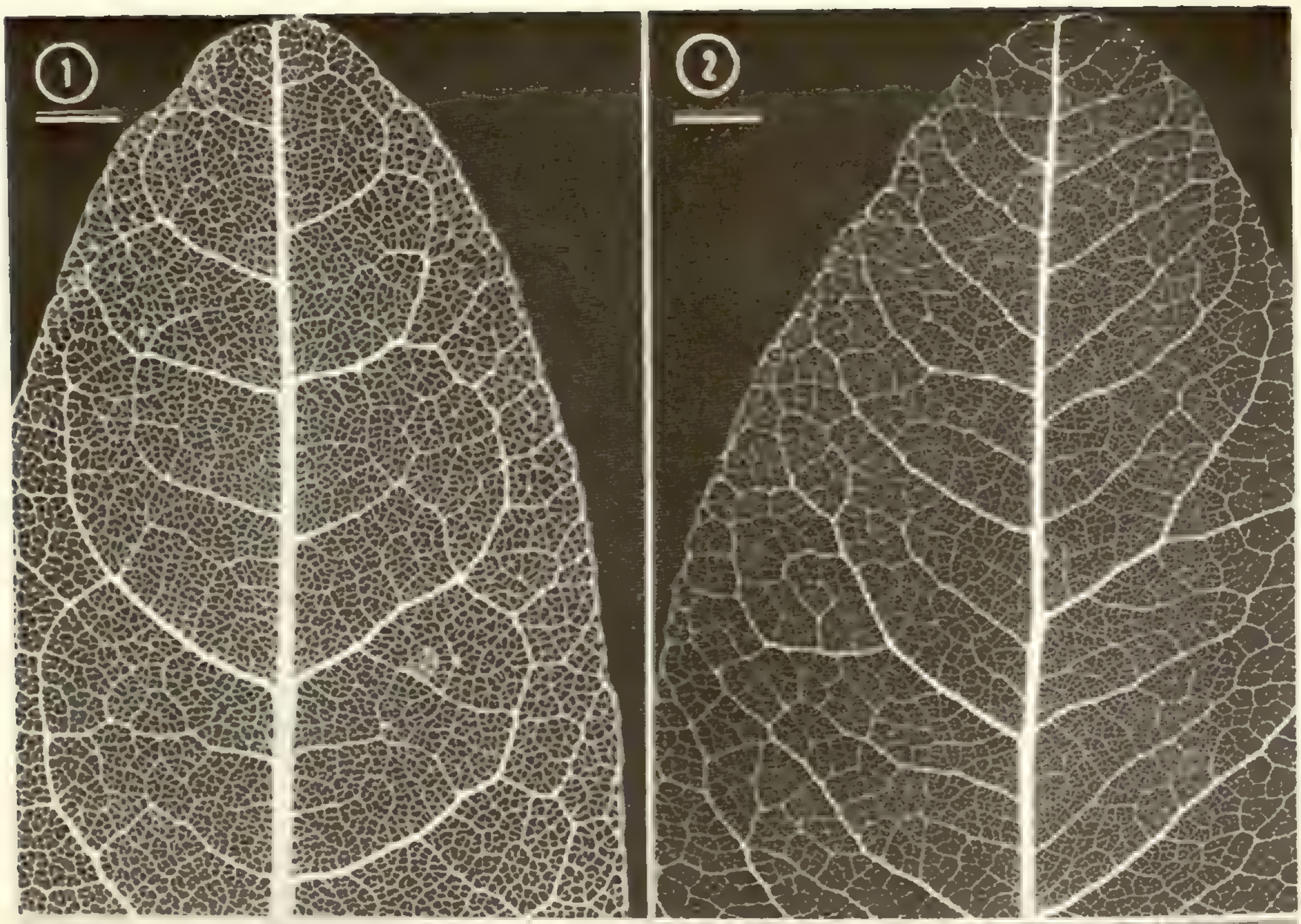
There are two layers of epidermal cells surrounding the petiole. The ground tissue external to the vascular tissue is similar to the cortex of the stem, and includes the same types of idioblasts. Groups of thick-

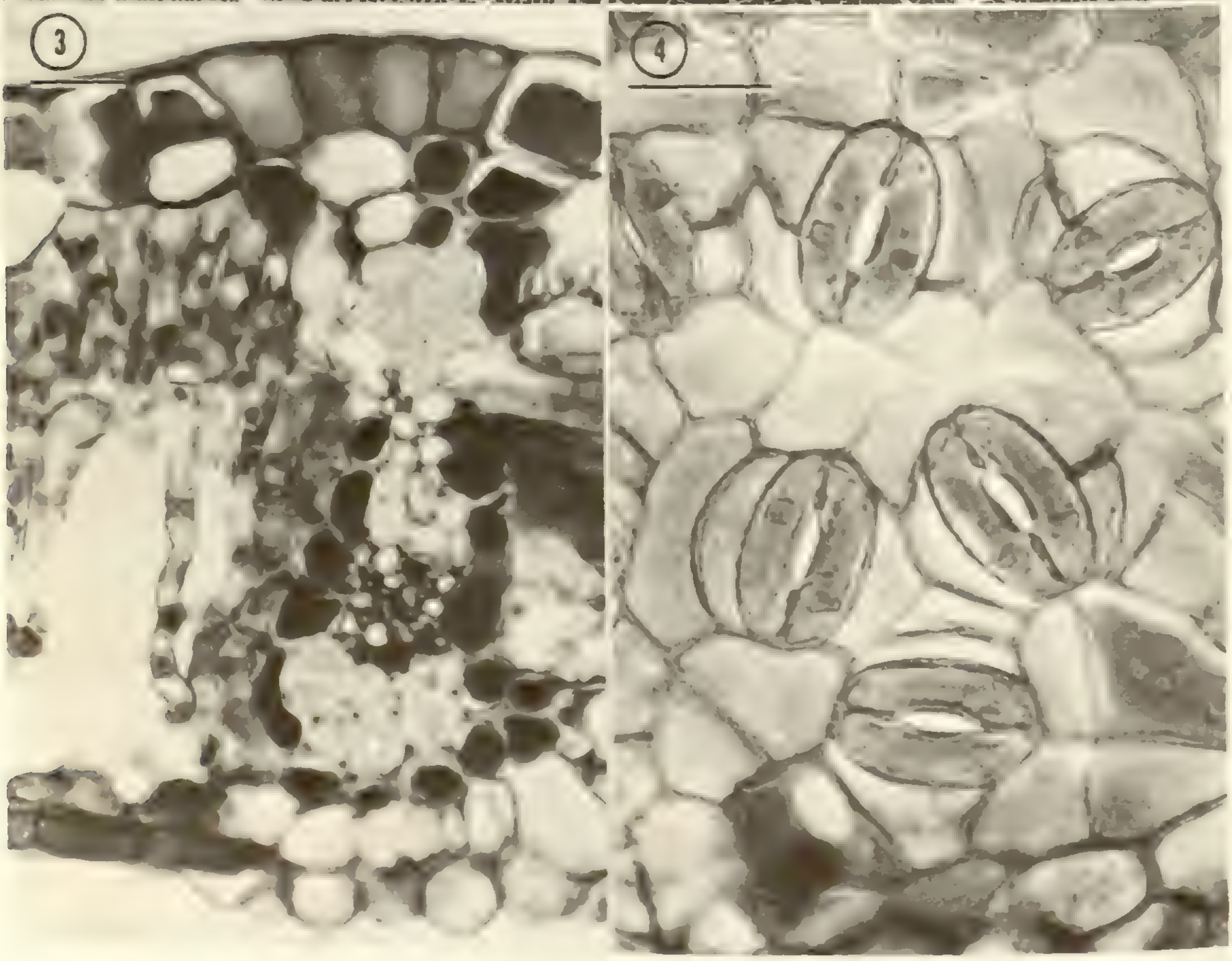
walled fibers form a discontinuous ring surrounding the vascular tissues. Phloem is external; xylem is internal. At the center of the petiole there are some sclerified parenchyma cells similar to the pith cells of the stem.

At the distal end of the petiole, the vascular tissues branch and enter the three leaflets. Mucilage cells become so numerous that they form the predominant cell type in the ground tissue surrounding the vascular tissues. In some instances portions of cell walls between adjacent mucilage cells are lacking, thus forming short (3–4 cells long) mucilage cavities. The groups of extraxylary fibers begin to disappear prior to the branching of the vascular tissue into individual vascular bundles. These fibers reappear in the petiolules. Five vascular bundles, three from the lower part and two from the upper part of the ring of petiolar vascular tissue, enter the petiolule of the middle leaflet. This results in two groups of vascular bundles located at opposite sides of the petiole; each of these groups of bundles enters the petiolule of a lateral leaflet. Within each petiolule the vascular bundles are arranged in the form of a broad U; this same vascular pattern is carried into the primary vein of the leaflet blade.

LEAF BLADE. Leaves of *Picrodendron* are trifoliolate. Leaflets have a smooth upper surface and entire margins. Thick-walled, unicellular trichomes are present on the abaxial surface, most frequently below the primary and secondary veins but with a few below higher order veins. Venation is pinnate; specifically, either brochidodromous or reticulodromous (FIGURES 1, 2). Areoles are well developed, random to partially oriented, and quadrangular to polygonal. Veinlets are simple, either linear or curved, or infrequently branched once. Marginal ultimate venation is fimbriate. Neither glands nor extrafloral nectaries are present.

The cuticle is thin, approximately 4 μm. thick over the primary vein and at the margin, and 2 μm. thick over the remainder of the laminar surface. Abaxially, the cuticle is thinner and sometimes difficult to detect. Both epidermides are uniseriate (FIGURE 3). Cells contain an amber-colored substance and, rarely, prismatic crystals. In surface view epidermal cells of both leaf surfaces are roughly squarish to rectangular (up to two or three times longer than broad) and mostly 15–35 μm. long. All walls are straight and smooth. In cross section, cells of the upper epidermis are roughly squarish to rectangular and 20–25 μm. tall; cells of the lower epidermis are similar, but only 10–15 μm. tall. Stomata are restricted to the abaxial surface. Subsidiary cells have their long axes parallel to the long axis of the pore, i.e., the stomatal apparatus is paracytic. Apparently a cell division may take place in subsidiary cells and, depending on the plane of division, the division results in paired subsidiary cells in two possible orientations on each side of the guard cells (FIGURE 4): if the plane of division is parallel to the long axis of the pore, the result is a pair of subsidiary cells with their long axes also parallel to the pore; if the plane of division is perpendicular to the long axis of the pore, the result is a pair of somewhat triangular cells adjacent to each guard cell. Guard cell pairs range from 27 to 34 μm. long and from 12 to 24 μm. wide,





FIGURES 1–4. **Picrodendron baccatum:** 1, leaflet clearing showing brochidodromous venation, *Gillis 10975*; 2, leaflet clearing showing reticulodromous venation, *Gillis 6963*; 3, cross section of leaflet showing a small vein with a bundle sheath and bundle sheath extension, *Gillis 10893*; 4, paradermal section of leaflet showing stomata and various configurations of subsidiary cells, *Gillis 10893*. Figs. 1, 2, bar = 2.5 mm.; Figs. 3, 4, bar = 20 μm.

and have an average length to width ratio of 1.58. Guard cell walls are unevenly thickened: the upper portion of the anticlinal wall adjacent to the pore and the inner periclinal wall are thickest; the lower portion of the anticlinal wall adjacent to the pore is somewhat thinner; and the remaining walls are only as thick as those of other epidermal cells. Typically a larger outer ledge and a smaller inner ledge of cuticle are present. Each guard cell is reniform, and guard cell pairs are elliptical in face view.

Leaflets are dorsiventral and possess a heterogeneous mesophyll (FIGURE 3). Palisade mesophyll cells are of different lengths and are arranged in 1–4 rows of cells. Most spongy mesophyll cells are elongated vertically and are situated near the veins, with very few cells present in the center of the areole. Consequently, very large intercellular spaces are formed between the veins. Some shorter and more "normal" looking spongy parenchyma cells are present in a thin layer near the lower epidermis.

In cross section, the primary vein possesses a semicircular arc of vascular tissue. Patches of conducting cells of the xylem separated by small groups of parenchyma cells are situated on the inner (adaxial) portion of the arc. Phloem is situated below the xylem on the outer (abaxial) portion of the arc. There are groups of thick-walled fibers external to the phloem and also between the two ends of the arc of vascular tissues, thus enclosing a pithlike region of parenchyma cells. These parenchyma cells have sclerified walls and may contain an amber-colored substance. Among the parenchyma cells of the ground tissue surrounding the vascular tissues of the midvein, there are idioblasts which may contain an amber-colored substance, mucilage, druses, or prismatic crystals. Druses, prismatic crystals, and cells containing an amber-colored substance are also found in the phloem.

Secondary and higher order veins are all vertically transcurrent (FIGURE 3). The xylem (adaxial) and phloem (abaxial) are situated between two groups of thick-walled fibers. Parenchymatous bundle sheath cells surround the conducting cells and the fibers. Cytoplasm and nuclei are evident in some bundle sheath cells; others contain an amber-colored substance or crystals. Veins are connected to both epidermides by a one- or two-cell-thick bundle sheath extension. The parenchymatous bundle sheath extension flares out near each epidermis to such an extent that it may be wider than the vein itself. Cells of the bundle sheath extension frequently contain druses or prismatic crystals.

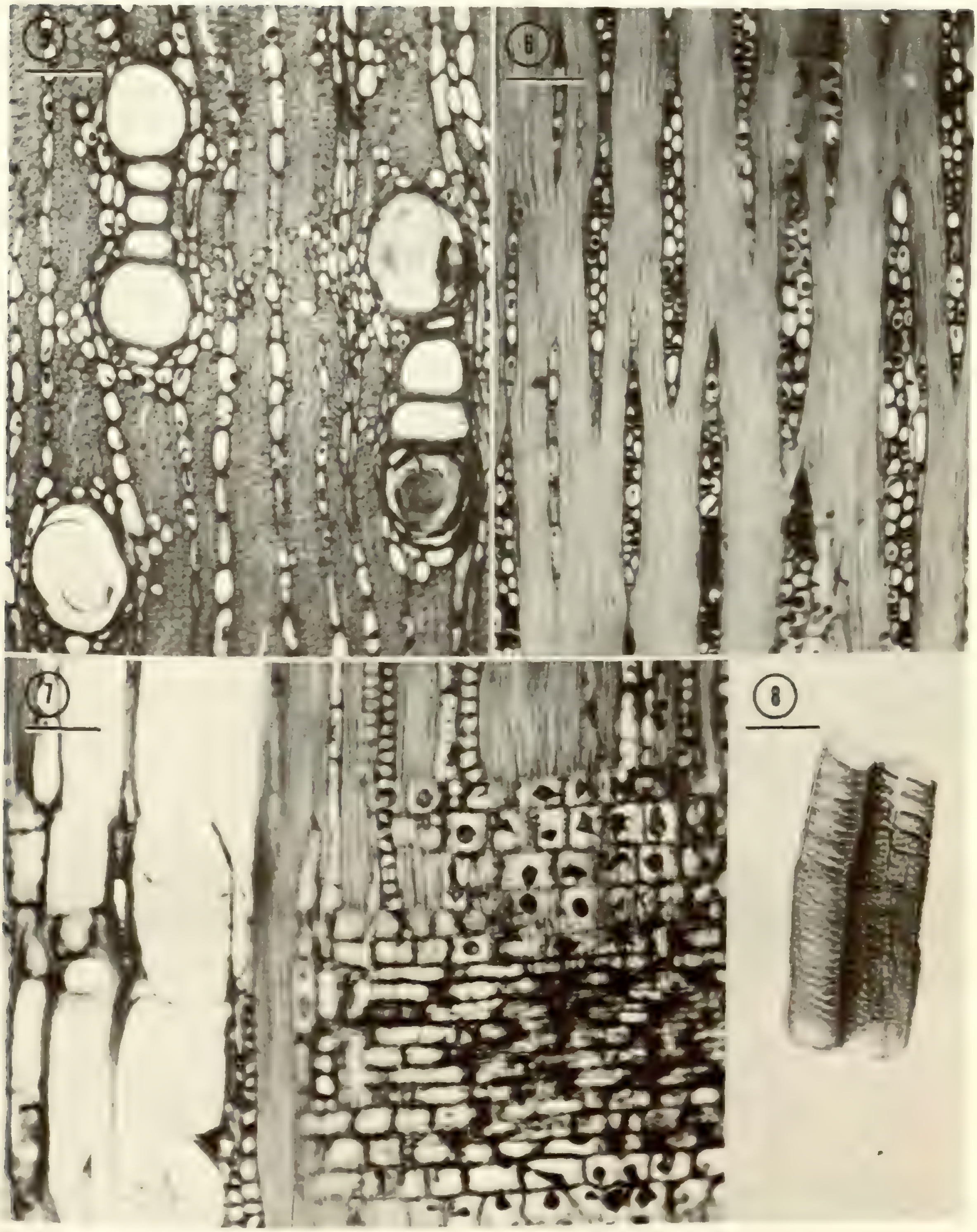
Ultimate veinlets do not possess fibers, phloem cells, or a bundle sheath extension to the lower epidermis. Such veinlets consist of a single row of xylem elements surrounded by a parenchymatous sheath, and are connected to the upper epidermis by a single row of parenchymatous bundle sheath extension cells. Within approximately 30 μm. of the termination of the veinlet, the upper bundle sheath extension is lost. The veinlet ends abruptly as a single xylem element surrounded by two parenchymatous bundle sheath cells.

WOOD. Distinct growth rings are not present in the wood of *Picrodendron*. Pores are distributed as follows: 62 percent solitary, 34 percent in radial multiples of 2–13 cells, and 4 percent in clusters of 3–10 cells (FIGURE 5). Pore outlines are circular or slightly elliptical. Vessel element walls have an average thickness of 5.2 μm. and a range of 3.0–7.5 μm. The moderately small pores have an average tangential diameter of 88 μm., with a range of 45–153 μm. Perforation plates are exclusively simple and have a narrow border. Intervascular pitting is alternate; the pits are circular to polygonal and show circular to elliptical inner apertures included within the pit border. Sometimes inner apertures of two adjacent pits coalesce, forming a groove on the inner surface of the vessel wall. Intervascular pits are medium-sized; average vertical diameter is 8.1 μm., with a range of 4.0–10 μm. The moderately short vessel elements (FIGURE 8) range from 124 to 494 μm. long, with an average length of 299 μm. Vessel elements are usually ligulate. Vessel element end wall angles range from 16 to 90°, with an average inclination of 57° from the vertical. Thin-walled tyloses were observed in sections of the heartwood; otherwise vessel elements are without deposits.

Imperforate tracheary elements have very thick walls and simple or faintly bordered pits with crossed inner apertures which are approximately 2.5–3.0 μm. long. These moderately short imperforate elements have an average length of 872 μm., with a range of 538–1700 μm. The very narrow lumen of imperforate tracheary elements frequently contains amber-colored deposits.

Rays are both uniseriate and multiseriate. Both types of rays are heterocellular, consisting of procumbent cells near the center of the ray and 1–3 rows of square to short erect cells at the margin of the ray (FIGURES 6, 7). Marginal ray cells are frequently disjunctive. Uniseriate rays average 16 μm. wide and 168 μm. (2–9 cells) high. Multiseriate rays are mostly biseriate, but there are some triseriate rays. Multiseriate rays average 30 μm. wide and 293 μm. tall. Multiseriate rays have uniseriate wings of 1–4 cells, and in some cases two superposed multiseriate rays may be connected by their uniseriate wings. Pit-pairs between ray cells and vessel elements vary from half-bordered to simple and have an average vertical diameter of 6.5 μm. The width of the pit-pairs varies from 5.4 to 11 μm., so the overall shape ranges from circular to elliptical. Ray cells frequently contain an amber-colored substance. No crystals were observed in ray cells.

The amount and distribution of axial xylem parenchyma varies somewhat in the different specimens examined, and even in different parts of the same specimen. Paratracheal parenchyma is mostly scanty, but sometimes vasicentric, or approaching aliform. Apotracheal parenchyma is diffuse, diffuse-in-aggregates, or in poorly or well-defined bands up to 10 cells wide. Axial xylem parenchyma cells are of two distinct sizes: tall cells (average height 67 μm.) and short cells (average height 23 μm.). Tall axial xylem parenchyma cells have contents similar to ray cells, whereas the short cells contain an anisotropic prismatic crystal and have



FIGURES 5–8. **Picrodendron baccatum:** 5, cross section of wood showing a solitary pore and two radial multiples, *Stadtmiller 171* (SJRW 19616); 6, tangential section of wood showing uni-, bi-, and triseriate heterocellular rays, *Stadtmiller 171* (SJRW 19616); 7, radial section of wood showing a heterocellular ray, *Stadtmiller 171* (SJRW 19616); 8, vessel elements from macerated wood, *Gillis 6963*. Figs. 5–8, bar = 80 μm.

sclerified walls. Strands of axial xylem parenchyma cells average 418 μm. long and may consist of 6–8 tall cells, 16–18 short cells, or an intermediate number of cells since both types of cells may occur in the same strand. Pits between vessel elements and xylem parenchyma cells are half-bordered.

DISCUSSION

Aside from a comparison of the anatomy given above with that contained in earlier literature, data on the anatomy of *Picrodendron* can be applied to two different taxonomic questions: Is there any anatomical evidence for more than one species in the genus? Moreover, what evidence does the anatomy of *Picrodendron* provide towards the elucidation of its relationships?

Comparisons with Earlier Anatomical Results

In several respects the results reported here differ from descriptions contained in earlier literature. Mucilage lacunae were not observed in the pith as reported by Jadin (1901), nor were mucilage cells observed in the mesophyll as reported by Boas (1913). Contrary to Metcalfe and Chalk (1950), I do not interpret the mesophyll as homogeneous since there are large intercellular spaces in the lower half of the mesophyll (Figure 3) which are not found among the palisade cells, and further, not all of the cells of the lower half of the mesophyll are vertically elongated. For these reasons I feel justified in calling the mesophyll heterogeneous.

Webber (1936) interpreted the imperforate tracheary elements in the wood of *Picrodendron* as libriform wood fibers, implying the presence of simple pits. My investigations show that pits on these elements are either simple or have a faint border. Therefore, I have joined Heimsch (1942) and Record and Hess (1943) in calling these cells merely imperforate tracheary elements, avoiding the difficult decision in distinguishing fiber-tracheids from libriform wood fibers in cases where the pits are only vaguely distinct.

Except for the presence of heterogeneous rays in wood of *Oldfieldia africana* specimen USW 19900 (Hayden, 1976), no other discrepancies were noted in Lebaq and Dechamps's (1964) description of this species. Likewise, specimens of *Oldfieldia*, *Celaenodendron*, *Piranhea*, *Irvingia*, *Klainedoxa*, and *Desbordesia* examined conform to descriptions in Record (1928, 1938), Webber (1936), and Metcalfe & Chalk (1950).

Infrageneric Variation

Woods of the four specimens of *Picrodendron* examined show only small differences among themselves such as variation in the amount and distribution of axial xylem parenchyma. Furthermore, in comparison with the specimens from cultivation in Florida, wood of the Haitian specimen has a coarser texture (larger cells), greater average multiseriate ray height,

and more frequent vertically fused rays. These variations are not surprising, and probably reflect little more than the common observation that wood specimens from the same species will vary with position in the stem, age, and the growing conditions under which the wood was formed.

Likewise, leaves of the specimens examined are quite similar anatomically. There is, however, one aspect of leaf architecture that might be construed as evidence for more than one species of *Picrodendron*. Leaflets may have brochidodromous or reticulodromous venation (FIGURES 1, 2). Collections at the U. S. National Herbarium show that both of these venation patterns are frequent in the genus. However, brochidodromous and reticulodromous venation patterns seldom occur together in a single species (Leo J. Hickey, pers. comm.). The presence of a fimbrial vein in leaflets of *Picrodendron* is significant in this regard, since the occurrence of this structure is frequently correlated with pronounced variability in the dromy of the secondary veins (Hickey, pers. comm.). Thus, leaf architecture does not provide any convincing evidence for more than one species in the genus.

Leaflet outline varies somewhat in the specimens examined. According to Gillis (pers. comm.), leaflet form varies considerably throughout the populations which he examined. Patterns of leaflet variation which Small (1917) used to characterize the three species can no longer be relied upon owing to the foliar diversity in the specimens accumulated since his time.

No significant differences were discerned in nodal and petiolar patterns among the specimens available. Nodal and petiolar data presented here also agree very closely with the results of Richard A. Howard (pers. comm.).

There is, then, no sound anatomical evidence which could be used consistently to distinguish three separate species in the genus *Picrodendron*. On the contrary, the specimens examined are remarkably homogeneous, with the exception of their leaf morphology.

RELATIONSHIPS OF PICRODENDRON

Aside from the families discussed below, *Picrodendron* has also been associated with Terebinthaceae (Hallier, 1908) and Bombacaceae (Hallier, 1923). Terebinthaceae, as delimited by Hallier (1908), consisted of some Simaroubaceae, Anacardiaceae, and Engler's Juglandales, among other groups, most of which are discussed separately below. Bombacaceae and *Picrodendron* have little in common. Since Hallier (1923) presented no evidence to support such an association, a detailed discussion of possible relationships with Bombacaceae seems unnecessary here.

Relationships with Juglandaceae

From the evidence presented below, it seems apparent that much of the resemblance between *Picrodendron* and Juglandaceae is merely superficial. Shared in common are compound leaves, male inflorescences springing

from the previous year's growth (only some Juglandaceae), female flowers containing a bicarpellate ovary with a 2-lobed style, drupaceous fruits (only some Juglandaceae), and exendospermous seeds with a superior radicle. The morphological differences between *Picrodendron* and Juglandaceae are, however, numerous, the latter typically having the following characteristics: stipules absent; male flowers with tepals and rudimentary ovary; female flowers subtended by bracts; ovary inferior, one loculed above and 2–4 below; ovules one per locule, basal, orthotropous, with a single integument (Lawrence, 1951; Hutchinson, 1973; Willis, 1973). Furthermore, the pollen of *Picrodendron* is quite different from that of Juglandaceae (Erdtman, 1952; C. Rose Broome, pers. comm.).

Picrodendron and Juglandaceae are also quite dissimilar anatomically. One of the most typical features of leaves in the Juglandaceae is the presence of several different kinds of hairs, either simple, unicellular or uniseriate, or tufted: capitate glandular hairs are found in *Juglans,* and peltate glands with short unicellular or uniseriate stalks are a constant and characteristic feature for the family. Stomata are anomocytic. The vascular system of the petiole and midvein may be variously shaped and oriented, but possesses additional vascular strands on the adaxial side of the main cylinder (Metcalfe & Chalk, 1950). Leaves of *Picrodendron,* with their simple unicellular hairs, paracytic stomata, and petiole and midvein with simpler vasculature, differ greatly from leaves in Juglandaceae. These differences are further emphasized by the vertically transcurrent minor veins and vertically oriented spongy mesophyll cells in *Picrodendron.*

Kribs (1927), Heimsch and Wetmore (1939), Heimsch (1942), and Metcalfe and Chalk (1950) have studied wood anatomy in the Juglandaceae. In general, these authors report fiber-tracheids as the groundmass in all genera, scalariform perforation plates in some genera, a tendency towards ring porosity in other genera, and parenchyma that is chiefly in bands, diffuse and diffuse-in-aggregates parenchyma being found in only a few species. These woods differ strongly from the wood of *Picrodendron,* which is characterized by thick-walled imperforate elements approaching libriform wood fibers, exclusively simple perforation plates, pores more or less evenly distributed, and abundant diffuse and diffuse-in-aggregates axial xylem parenchyma.

On the basis of floral morphology, palynology, and anatomy, one must conclude that there is very little evidence for a relationship between *Picrodendron* and Juglandaceae.

Relationships with Simaroubaceae and other "Pinnatae"

It will be recalled that *Picrodendron* has been associated with the Sapindaceae, Anacardiaceae, Simaroubaceae, and Burseraceae. These families, along with Rutaceae and Meliaceae, comprise a conspicuous portion of a group of plants which Hutchinson called the "Pinnatae" (see Rock, 1972, for discussion of the placement of these families in various systems of

classification). This group of chiefly woody plants, as its name implies, is characterized by pinnately compound leaves. *Picrodendron*, with its trifoliolate leaves, resembles at least superficially many "Pinnatae." There are additional similarities in wood structure. Rock's (1972) survey of selected woods of this group points out the following characteristics: simple perforation plates, alternate intervascular pitting, imperforate tracheary elements with slit-like simple to slightly bordered pits, and "widespread presence of dark-staining, gum-like substances in the parenchyma and vessels . . ." In a discussion of five of these families (Sapindaceae was not included), Webber (1941) also noted vessel to ray pit-pairs that are in part half-bordered, and strands of crystalliferous parenchyma in many of these woods. Heimsch (1942) also noted many of the same characters in these families. The same features are also typical of *Picrodendron*, and this fact, together with its habit and frequent secretory cells (idioblasts) in the cortex, may indicate some sort of relationship between *Picrodendron* and the "Pinnatae."

Together, the six families of "Pinnatae" mentioned above account for about 6000 species of plants with various kinds of woody habits and floral structures. Because of the great number of plants involved, it is not difficult to find in diverse members of the "Pinnatae" floral features similar to many (but not all) of the features of *Picrodendron*. For example, plants with unisexual flowers or a reduced perianth or drupaceous fruits can be found in some parts of all "Pinnatae" families. Even an obturator can be found in Anacardiaceae and Meliaceae; the significance of this fact is not easily interpreted since, according to Davis (1966), in Anacardiaceae the obturator is of funicular origin and in Meliaceae, while of placental origin, it is composed of hairlike cells unlike the obturator of *Picrodendron*. It should be emphasized that these features are not constant, and that many "Pinnatae" are characterized by a biseriate perianth, bisexual flowers, various fruit types, and a lack of obturators. Further, some "Pinnatae" possess specialized features not found in *Picrodendron*: the lianous habit and peculiar stipules of some Sapindaceae; the zygomorphic floral symmetry in some Anacardiaceae, Rutaceae, and Sapindaceae; the staminal tube typical of Meliaceae; and the pellucid-punctate glandular leaves of the Rutaceae. Certainly the indefinite number of stamens in the male flowers and the absence of a floral disc in the flowers of both sexes of *Picrodendron* can be considered as evidence against a relationship to "Pinnatae."

Some outstanding anatomical differences between *Picrodendron* and "Pinnatae" include: secretory canals in the cortex, pith, or bark of various Anacardiaceae, Simaroubaceae, and Sapindaceae; secretory canals in the wood rays of many Anacardiaceae and Burseraceae; and the predominance of anomocytic stomata throughout most of the "Pinnatae" families under consideration. Secretory canals of either type are absent, and stomata are paracytic in *Picrodendron*. Before reaching any final conclusions about relationships with the "Pinnatae," one should consider the Simaroubaceae

in greater detail because so many botanists have placed *Picrodendron* in or adjacent to this family.

When associated with the Simaroubaceae, *Picrodendron* is usually considered closest to three genera from tropical Africa and Southeast Asia; namely, *Irvingia* Hooker f., *Klainedoxa* Pierre, and *Desbordesia* Pierre ex van Tieghem. If these three genera are retained in Simaroubaceae, they comprise the well-defined subfamily Irvingioideae Engler. Alternatively, some authors (e.g., Hutchinson, 1973) place these genera in the family Irvingiaceae [2] van Tieghem, while others (e.g., Willis, 1973) place them in the Ixonanthaceae [2] Planchon ex Klotzsch, a small family having affinities with the Linaceae.

One can only guess why Planchon (1846) associated *Picrodendron* with the Simaroubaceae in the first place. Nevertheless, once it was placed in this family, numerous anatomical similarities to the Irvingioideae were discovered, thus strengthening the association despite the many morphological differences between *Picrodendron* and this subfamily. Anatomical characters in common are paracytic stomata, palisade-like spongy mesophyll, vertically transcurrent minor veins, mucilage cells or spaces in the cortex, and frequent crystals in the stem and leaf (Jadin, 1901; Solereder, 1908; Boas, 1913; Metcalfe & Chalk, 1950). On the other hand, *Picrodendron* lacks mucilage cells in the pith which are found in *Irvingia* and its allies. Members of Irvingioideae differ from *Picrodendron* in having the following morphological characters: simple leaves, very large stipules, two perianth whorls, bisexual flowers, a floral disc, a definite number of stamens (10), 5–4 carpels (but *2* in *Desbordesia*), an undivided style, and only one ovule per locule (Hutchinson, 1973).

The woods of *Picrodendron* and *Irvingia* and allies (as well as the euphorbiaceous woods discussed herein) are also quite similar. These woods are characterized by vessel elements with simple perforation plates, alternate intervascular pitting, ray to vessel and/or parenchyma to vessel pit-pairs ranging from half-bordered to simple, at least some parenchyma in bands, very thick-walled imperforate tracheary elements with simple or faintly bordered pits, multiseriate rays often vertically fused, parenchyma cells frequently filled with an amber-colored substance, and sclerified, crystalliferous, axial xylem parenchyma cells.

However, despite these overall similarities, the woods of *Irvingia*, *Klainedoxa*, and *Desbordesia* form a distinct and presumably natural group. When they are compared with *Picrodendron*, the most noticeable difference is the coarser texture of these woods: pores are mostly moderate-sized to rather large (tangential diameter ranges from 114 to 285 μm.), vessel ele-

[2] According to ICBN (1972), Appendix II, Nomina Familiarum Conservanda, the proper authorities for the family names Irvingiaceae and Ixonanthaceae are Exell and Mendonça, presumably the first to use the names in the proper form for families. The references as given on page 230 of the Code are: **Irvingiaceae** Exell et Mendonça, Consp. Fl. Angol. **1**: 279, 395. 1951 [Pierre, Bull. Mens. Soc. Linn. Paris **2**: 1233. 1896 (*'Irvingiacées'*)], and **Ixonanthaceae** Exell et Mendonça, Bol. Soc. Brot. ser. 2a. **25**: 105. 1951 [J. E. Planchon ex Klotzsch, Abh. Königl. Akad. Wiss. Berlin **1856**: Phys. Abh. 235. 1857 (*'Ixionantheen'*)]. ***Ed.***

ments are mostly long (500–685 μm.), and imperforate tracheary elements (1368–2800 μm.) are medium-sized to very long (Webber, 1936). In addition, unilaterally compound pitting is often present between vessel elements and parenchyma cells, rays are somewhat broader, and ray cells are nearly all procumbent with a single row of square cells at the margin of the ray in the woods of Irvingioideae (Webber, 1936). Most of these differences, though, are merely details, and one must conclude that, as a group, *Picrodendron* and *Irvingia* and its allies are anatomically more homogeneous than are members of some well-defined and so-called natural families. (Compare, for example, the structural diversity present in Juglandaceae as mentioned above.)

As far as the relationships of *Picrodendron* are concerned, *Irvingia*, *Klainedoxa*, and *Desbordesia* pose a difficult problem since, on the one hand they are quite like *Picrodendron* anatomically and, on the other hand, they are markedly different morphologically. Because concepts of plant relationships are based primarily on floral morphology, it seems prudent in this case not to overweight the importance of anatomical evidence. Furthermore, *Irvingia* and its relatives are found exclusively in the Old World. In the absence of any other evidence for a relationship between members of the Irvingioideae and *Picrodendron*, it seems possible that the anatomical similarities of these plants are the result of convergent evolution. On the other hand, Webster (1967, and pers. comm.) thinks the Irvingioideae may be distantly related to Euphorbiaceae and, hence, also distantly related to *Picrodendron* (see below). Other subfamilies of the Simaroubaceae are even more different from *Picrodendron* than the Irvingioideae, both anatomically (Webber, 1936) and on the basis of floral morphology (Cronquist, 1944).

As far as a relationship to the "Pinnatae" in general is concerned, the position of *Picrodendron* is unclear. While its characters fall within the range of diversity of the "Pinnatae," *Picrodendron* would be a rather anomalous element of any family in the "Pinnatae" in which it might be placed. Differences do not seem too great, however, to preclude placing *Picrodendron* in its own family near or among the families of "Pinnatae," as was done by Scholz (1964) and by Takhtajan (1966).

Relationships with Euphorbiaceae

Fawcett and Rendle (1917) were first to propose a relationship between *Picrodendron* and Euphorbiaceae, saying, "The presence and form of the obturator at once suggested the family Euphorbiaceae and this affinity is borne out by other floral characters." Pax and Hoffmann (1931) excluded *Picrodendron* from Euphorbiaceae on the basis of its ovary (which they mistakenly thought to be inferior), lack of endosperm, and folded cotyledons. Palynological studies have largely been responsible for rekindling interest in a possible relationship between *Picrodendron* and Euphorbiaceae (Erdtman, 1952; Novák, 1961). Palynology has also proven useful in indicating affinities within the Euphorbiaceae; on this basis *Picroden-*

dron seems closest to the subfamily Oldfieldioideae Köhler & Webster (Webster, 1967 and 1975). Pollen of *Picrodendron* and certain genera of Oldfieldioideae are remarkably similar when viewed with either a scanning or a transmission electron microscope (Broome, pers. comm.).

Flowers of *Picrodendron* resemble those of the Euphorbiaceae more than those of its other putative relatives (see TABLE 2). Although the bicarpellate ovary, absence of a floral disc, and exendospermous seeds of *Picrodendron* are departures from "typical" Euphorbiaceae, these features are not unknown in the family. The pendulous, anatropous ovules with a placental obturator and the ventral raphe of *Picrodendron* present perhaps the strongest argument for its inclusion in the Euphorbiaceae, since this configuration is reputed to be the most constant and characteristic feature of Euphorbiaceae (Willis, 1973). *Picrodendron* is biovulate and has spinulose pollen, hence an affinity to the Oldfieldioideae seems likely. Although members of the Oldfieldioideae have diverse habits, *Celaenodendron* and *Piranhea* are trees with trifoliolate leaves which have a general resemblance to *Picrodendron*.

Relatively little is known about the anatomy of members of the Oldfieldioideae, unlike that of other putative relatives of *Picrodendron*. Metcalfe and Chalk (1950) examined only the primary structure of *Micrantheum* Desf., *Stachystemon* Planchon, and *Petalostigma* F. Mueller among the Oldfieldioideae. They mention very little specifically about these plants, all of which are Australian. The former two are ericoid in habit which is no doubt associated with anatomical specializations not necessarily characteristic of the trees and shrubs that make up most of the Oldfieldioideae. Nevertheless, paracytic stomata, vertically transcurrent small veins, and so-called "tanniniferous" cells occur commonly in the Euphorbiaceae (Metcalfe & Chalk, 1950) as well as in *Picrodendron*.

Metcalfe and Chalk (1950) examined seven genera of the Oldfieldioideae for wood structure. In general, these woods are characterized by simple perforation plates, alternate intervascular pitting, thick-walled fibers, heterogeneous rays mostly 2 or 3 cells wide, and banded and/or diffuse axial xylem parenchyma with some chambered crystalliferous cells, all of which are also typical of *Picrodendron*. Woods of *Picrodendron* and *Oldfieldia* are remarkably similar (Hayden, 1976). Aside from the similarities mentioned above and in the discussion of *Irvingia* and its allies, *Picrodendron* and *Oldfieldia* share the following characteristics: solitary pores about twice as frequent as radial multiples, pore clusters present only infrequently, intervascular pits which may have coalescent inner apertures, very similar heterocellular rays with some disjunctive cells, and multiseriate rays sometimes vertically fused. Furthermore, dimensions other than lengths of elements are similar in these woods. In contrast to the similarity between wood structures of *Picrodendron* and *Oldfieldia*, woods of *Celaenodendron* and *Piranhea* are more different. *Celaenodendron*, with its growth rings and small pores in predominantly long radial multiples, is distinctive. Both *Celaenodendron* and *Piranhea* have rays which are more homogeneous than those of *Picrodendron* or *Oldfieldia*, there being only a single row of

TABLE 2. **Comparison of salient morphological features of Picrodendron and Euphorbiaceae.**

	Picrodendron	Euphorbiaceae
SEXUALITY OF FLOWERS	unisexual	unisexual
DISC	absent	present, usually
SEPALS	0 or 5	0 or 5
PETALS	0	0 or 5
STAMENS	3–many	1–many
OVARY	superior	superior
LOCULES	2	3, usually
OVULES	2/locule pendulous anatropous	1 or 2/locule pendulous anatropous
RAPHE	ventral	ventral
CARUNCLE OR OBTURATOR	present	present
FRUIT	drupe	schizocarpous capsule, more rarely a drupe
ENDOSPERM	none	present, usually

square or short erect cells at the margin. Bands of parenchyma are more pronounced in some specimens of *Piranhea* than in *Oldfieldia*, *Picrodendron*, or *Celaenodendron*. Differences between the woods of *Picrodendron* and *Oldfieldia* and those of *Celaenodendron* and *Piranhea* are nevertheless far outweighed by the similarities.

The pollen and wood structure of *Picrodendron* are so similar to those of *Oldfieldia* that one might expect these genera to be closely related. Unlike *Picrodendron*, however, *Oldfieldia* has opposite, digitately compound leaves and rather different inflorescences, flowers, and fruits. (Compare, for example, illustrations of these genera in Hutchinson, 1969).

CONCLUSION

In view of the basically euphorbiaceous structure of the flowers of *Picrodendron* and the numerous similarities of its wood anatomy and pollen to those of *Oldfieldia* and the Oldfieldioideae in general, this subfamily of Euphorbiaceae probably contains the closest living relatives of *Picrodendron*. Placing *Picrodendron* in the Euphorbiaceae-Oldfieldioideae would thus be preferable to aligning it with either Juglandaceae or any family of "Pinnatae." These conclusions are based upon evidence from three different and independent lines of investigation. Because of the dissimilar morphology of *Picrodendron* and *Oldfieldia*, and in agreement with Web-

ster (1975), these genera are probably best placed in separate tribes of Oldfieldioideae.

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APPENDIX 1. **Additional notes concerning Picrodendron specimens used in this investigation.**

1) *Gillis 10893* — Collected by *David Fairchild* and *P. H. Dorsett 2846* on the Allison V. Armour Expedition; native of Jamaica, but collected from cultivation in Botanical Garden, Trinidad. P.I. 98559, M 5850.

2) *Gillis 10975* — Originally from seeds introduced by John Popenoe from Driggs Hill, South Andros, Bahamas; now plants with FTG #65–671; also *Gillis 11031* at FTG.

3) *Gillis 6963* — Cultivated on the estate of Mrs. Alvin Jennings, Coral Gables, Florida; source not known.

4) *Stadtmiller 171* (SJRW 19616) — This specimen, apparently unvouchered, was sent to Samuel J. Record at Yale through Mr. Stadtmiller from Service Technique du Département de l'Agriculture, Haiti, in 1931. A sample of this material was sent to Irma Webber in 1934 and is presumably that used in her "Systematic Anatomy of the Simarubaceae" (1936).

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FOSSIL DICOTYLEDONOUS WOODS FROM YELLOWSTONE NATIONAL PARK

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TWO REGIONS OF YELLOWSTONE NATIONAL PARK contain successive horizons of silicified tree trunks, many in upright position, preserved in volcaniclastic rocks. The spectacular sequence of more than 25 forests at Specimen Ridge and Amethyst Mountain, along the south bank of the Lamar River in the northeastern region of the Park, was discovered by Holmes about a century ago. These fossil forests have been described by several authors including Knowlton (1899) and Dorf (1960, 1964). The lesser known but equally striking succession of fossil forests in the northwestern Gallatin area has been described by Andrews (1939) and Andrews and Lenz (1946). The fossil forests in the two areas, more than 40 miles apart, are in beds of approximately equivalent ages.

More than 100 species of fossil plants, 75 percent of them dicotyledonous, have been identified (Dorf, 1960, 1964) from beds along the Lamar River, chiefly from leaves in finer sediments of the formation containing the fossil forests. This leaf flora has predominantly warm-temperate and subtropical affinities but includes some forms with modern relatives in the tropics. Although the broad climatic implications of this Yellowstone flora are clear, MacGinitie (1974) has pointed out that Knowlton (1899) designated many of the fossil plants by names that are stratigraphic rather than botanical, and that, despite some updating by Dorf (1960), the Yellowstone flora is in need of revision. Consequently, the systematic affinities of many Yellowstone dicotyledonous plants remain in doubt.

Warmer climatic conditions than were probable for the Yellowstone fossil flora are suggested by the Kisinger Lakes flora (MacGinitie, 1974) from beds of similar age some 80 miles to the southeast in the Wind River Basin, Wyoming. This flora apparently lacks close botanical similarity to the Yellowstone fossil flora.

Despite the dominance of angiospermous taxa in the Yellowstone leaf flora, coniferous wood is more abundant than hardwoods in the fossil forests. Both types of wood have been described by Felix (1896), Knowlton (1899), Platen (1908, 1909), and Beyer (1954); Conard (1930), Read (1930), and Andrews (1939) described only conifers. Like the leaf flora, the Yellowstone dicotyledonous woods need re-examination. Only three of them have been studied in the last half-century (Beyer, 1954).

To investigate the identity of the angiospermous plants in the Yellowstone fossil forests, one of us (Scott) has made collections of dicotyledonous woods from Specimen Ridge and Amethyst Mountain along the Lamar River, and in the Gallatin area. To avoid harm to the remains of trees in place, only detached pieces were obtained from the slopes; conse-

quently, the collections represent a generalized composite, both vertically and horizontally, of the trees from the many forest levels. The localities are designated as follows:

U.S.G.S. Paleobot. Loc. No. D2054A. Amethyst Mountain, Yellowstone National Park, Wyoming. Wood collected in Lamar River Formation from north and east facing slopes about 3 miles southwest of the intersection of Soda Butte Creek and the Lamar River about 400 to 1400 feet above river level. See Tower Junction (GQ-1247) Quadrangle, Wyoming-Montana, and Abiathar Peak (GQ-1244) Quadrangle, Wyoming, 1975.

U.S.G.S. Paleobot. Loc. No. D2054B. Specimen Ridge, Yellowstone National Park, Wyoming. Wood collected along north facing slopes in Lamar River Formation about 2 miles south and about 1000 to 1400 feet above the Lamar River from about 4 to 7 miles east of Tower Junction. See Tower Junction (GQ-1247) Quadrangle, Wyoming-Montana, 1975.

U.S.G.S. Paleobot. Loc. No. D2089. Gallatin Fossil 'Forest, Yellowstone National Park, Montana. Wood collected between 8000 and 9200 feet elevation on the south flanks and spurs of Big Horn Peak, at the head and on the ridges 1 to 3 miles upstream (to the northeast) along an unnamed tributary that joins Specimen Creek about 2 miles northeast of the mouth of Specimen Creek at the Gallatin River. See Crown Butte, Montana, 15′ Quadrangle, U.S.G.S. 1955.

More than 30 types of dicotyledonous woods have been recognized in our collections from the Lamar River and Gallatin fossil forests. These will be described in a series of papers: systematic descriptions will be included in the first papers, while most ecological and floristic discussion will be reserved for the final one.

GEOLOGIC OCCURRENCE AND AGE

The Lamar River and Gallatin fossil forests occur in strata of the Absaroka Volcanic Supergroup in the Absaroka volcanic field, developed during Eocene time over some 9000 square miles in northwest Wyoming and southwest Montana. This large field, studied recently by Smedes and Prostka (1972), consists of a number of stratovolcanoes and the air and water-deposited materials derived from them. The rocks in the vent areas consist of a chaotic assemblage of lava flows, autoclastic flow breccias, avalanche debris, mudflows, and tuffs. Alluvial facies consisting of well-bedded, reworked volcanic sediments grade outward from and interfinger with rocks of the vent facies, forming the rock units included in the Absaroka Volcanic Supergroup. The Gallatin fossil forest occurs in one such unit, the Fortress Mountain Member of the Sepulcher Formation. This formation grades laterally southeastward into the Lamar River Formation, the basal volcaniclastic unit throughout much of the northeastern portion of the Park. The Lamar River Formation contains both the Specimen Ridge and Amethyst Mountain fossil forests.

At the Amethyst Mountain fossil forest, the north- and east-facing

beds of the Lamar River Formation are overlain unconformably by the Eocene Langford Formation, which extends from elevations of about 8500 feet to cap Amethyst Mountain. The Langford Formation, lighter in color than the Lamar River Formation, contains very little fossil wood in this area (H. J. Prostka, pers. comm., March 30, 1976).

Events leading to the preservation of vertical sequences of forests in both the Sepulcher and Lamar River Formations appear to be similar. Volcanic materials now a part of these formations overwhelmed, buried, and contributed to the rapid silicification of the forests growing on the series of transitory soil surfaces which developed as the formations accumulated.

A potassium-argon age determination from the lower part of the Sepulcher Formation gave an age of 49.2 $\pm$ 1.5 m.y. (J. D. Obradovitch, in Smedes & Prostka, 1972). A similar late early to early middle Eocene age is indicated for the Lamar River Formation, which grades laterally into the Sepulcher Formation. This radiometric age determination is consistent with the age inferred for the Lamar River fossil leaf flora by Dorf (1960).

SYSTEMATIC DESCRIPTIONS

Many named species of fossil woods are placed by custom in genera whose names include a categorical suffix, now usually "-oxylon." For Tertiary woods having affinities with modern plants, such generic names are formed by adding this suffix to the name of the modern taxon, usually the genus, to which the fossil form appears to be most closely related. Such "-oxylon" genera are not required by the International Code of Botanical Nomenclature, whose preamble states that "The purpose of giving a name to a taxonomic group is not to indicate its characters or history, but to supply a means of referring to it and to indicate its taxonomic rank." (Stafleu *et al.*, 1972). Some examples of misleading names that have arisen through error or loose circumscription in the application of this convention are given by Lakhampal and Dayal (1968).

Despite some shortcomings, the apparent neatness of this approach to fossil wood nomenclature has led some students of Tertiary dicotyledonous woods (e.g. Kramer, 1974a) to feel that all named species of fossil woods should be assigned to organ and form genera whose names include the "-oxylon" suffix. Müller-Stoll and Mädel (1967) even consider that it is improper to assign an extinct species based on fossil wood to an extant genus. We find this approach extreme; it is certainly inconsistent with the practice of most paleobotanists when naming the majority of such detached plant parts as leaves, fruits, and seeds of Tertiary age.

In examples in which the fossil wood species falls clearly within the structural limits of a single modern genus, relative age rather than details of anatomy inevitably becomes the operative factor in delimiting the equivalent "-oxylon" genus. Schopf (1969) points out that a truly disjunct range in time is an impossibility for any group that has phyletic

unity. Because phyletic unity, as demonstrated by common morphology, is the reason for the choice of the modern base name for the "-oxylon" genus, age difference alone seems at best a dubious criterion for the establishment of that "-oxylon" genus. In such cases, encumbering existing nomenclature for the sake of uniformity in applying an informal convention seems to us only to obscure the contribution made by the fossil material to the geologic history of the genus. Consequently, in this series of papers, those fossil wood species whose anatomical features we regard as consistent with those of a single modern genus will be assigned to that genus.

Betulaceae

Alnus latissima Wheeler, Scott, & Barghoorn, sp. nov. Figures 1–3.

Growth rings. Present, distinct, 7–10 mm. wide.

Vessel elements. Diffuse porous, little or no change in vessel diameter and density throughout growth ring; tangential diameter 38–85 μm., mean 55 μm.; solitary and in radial multiples of 2–4 (rarely 5), a few clusters; density 70–136 per square mm.; perforation plates exclusively scalariform with 13–26 bars; intervascular pitting opposite and alternate, 5–6 μm. across; length 440–1045 μm.

Rays. Uniseriate and aggregate; homocellular; uniseriate rays 4–34 (48) cells; 92–760 μm. (1045 μm.) high.

Material. One specimen of silicified, mature secondary xylem, 45 $\times$ 55 $\times$ 48 mm.

Holotype. U.S.G.S. Fossil Wood Collection No. D2089–13. The species is named with reference to the unusually wide growth rings.

Locality. Gallatin Fossil Forest: U.S.G.S. Paleobot. Loc. No. D2089.

A number of salient features of the fossil indicate that it is a species of *Alnus*: small vessels solitary and in radial multiples, aggregate and uniseriate homocellular rays, scalariform perforation plates, and both alternate and opposite intervascular pitting. The somewhat similar woods of *Alnus* and *Betula* are separable on the basis of various characters. Both opposite and alternate intervascular pitting occur in *Alnus*; only alternate pitting occurs in the mature wood of *Betula*. Exclusively uniseriate rays occur in *Alnus*; multiseriate rays occur in *Betula* (Hall, 1952). Within *Alnus*, the fossil species with its aggregate rays does not belong to the section Alnobetula in which such rays are lacking, but it is not possible to determine with which of the other two sections it may have affinities. Only one species of the section Cremastogyne and none of the section Clethropsis were available for study (Hall, 1952).

The Yellowstone wood has wider growth rings (7–10 mm.) than have been reported for extant species of *Alnus*, but it is otherwise indistinguishable from extant members of the genus. One specimen of *Alnus acuminata*

(Hw 19514) from Argentina differs from species of *Alnus* from more northerly regions, as it lacks distinct growth rings and has thinner-walled, larger imperforate elements and a lower vessel density.

In North America pollen and foliage of *Alnus* are known from Late Cretaceous and younger rocks (Wolfe, 1973). Pollen of *Alnus* is reported from the Kisinger Lakes flora (Leopold, in MacGinitie, 1974) and from the fossil forest beds in Yellowstone National Park (Fisk & DeBord, 1974). However, to the best of our knowledge this is the first fossil wood of *Alnus* described from the Tertiary of North America. There are two reports of *Alnus* wood from the Pliocene of Austria and Germany (Müller-Stoll & Mädel, 1959) and one from the Tertiary of Rumania (Petrescu & Nuta, 1969). *Alnus* occurs on all continents of the Northern Hemisphere; it extends southward in Asia to Assam and in the New World through Mexico and Central America. In the Andes the genus ranges to Peru, Bolivia, and northern Argentina (Willis, 1973).

Carpinus saximontana Wheeler, Scott, & Barghoorn, sp. nov.
FIGURES 4, 5.

Growth rings. Distinct; wavy in outline; 5–16 mm. broad.

Vessel elements. Solitary, in radial multiples of 2–14, or rarely in pore clusters; tangential diameter in early wood 32–87 μm., tangential diameter in late wood 23–60 μm.; gradually decreasing in diameter through the growth ring, longest radial multiples in late wood; length 550–780 μm.; perforations simple; intervascular pitting alternate, medium, angular due to crowding; pits to ray parenchyma oval; slightly bordered; tyloses thin-walled, infrequent.

Parenchyma. Difficult to see in cross section; in longitudinal section strands of 10 or more cells observed; apparently apotracheal diffuse; cells slightly inflated, occasionally crystalliferous.

Rays. 1 and 2 cells wide and aggregate, aggregate rays widely spaced; homocellullar; biseriate rays 10–48 cells, 110–920 μm. high; uniseriates 3–17 cells, 55–276 μm. high.

Imperforate tracheary elements. Thin-walled; length and pitting not observed.

MATERIAL. Three specimens of silicified, mature secondary xylem, the type specimen measuring 90 × 48 × 65 mm.

HOLOTYPE. U.S.G.S. Fossil Wood Collection No. D2089–16. The species name refers to the Rocky Mountains, where this taxon constitutes the first Eocene record.

LOCALITY. Gallatin Fossil Forest: U.S.G.S. Paleobot. Loc. No. D2089.

The combination of features present in this fossil wood (aggregate rays accompanied by uniseriate and biseriate rays, alternate intervascular pitting, and small vessels occurring in radial multiples) is characteristic of

the Betulaceae. *Carpinus* is the only genus in the family that contains species with both aggregate rays and predominantly simple perforation plates; thus, the fossil is assigned to this genus. *Carpinus* includes two sections, CARPINUS, with predominantly or exclusively simple perforation plates, and DISTEGOCARPINUS, with exclusively scalariform perforation plates. The simple perforation plates of this fossil *Carpinus* wood ally it with the section CARPINUS.

Hall (1952) describes the vessel arrangement in *Carpinus* as diffuse porous, and his figured specimens show relatively uniform vessel size and distribution within a growth ring. According to Hall, growth rings in *Carpinus* range in width from 125 μm. to 4 mm. In the Yellowstone fossil *Carpinus*, there is a more conspicuous change of vessel size and distribution within a growth ring, and the growth rings are 5 to 16 mm. wide. However, a specimen of modern *C. caroliniana* Walter (Hw 9857) with wide growth rings (5–7 mm.) showed changes in vessel diameter and distribution comparable to those in the fossil *C. saximontana*. Slides of six specimens of *C. caroliniana* Walter were examined; differences among these specimens are as great as the differences among some of the other ten species of the genus examined.

Carpinoxylon ostryopsoides Page (1970) from the Upper Cretaceous of California is the only other North American fossil wood that can be assigned with confidence to the tribe Coryleae. This wood has "flamelike" vessel distribution, a feature of *Ostryopsis* and *Corylus*. *Carpinoxylon pfefferi* Platen (1908) was described from the Auriferous Gravels of California, but Müller-Stoll and Mädel (1959) believe that the specimen is not betulaceous as the rays are heterocellular and up to 14 cells wide.

Wood of *Carpinus* is not common in the fossil record. In their comprehensive review of fossil woods of the Betulaceae, Müller-Stoll and Mädel (1959) list only four species: two from Europe, one from the Sahara, and one from Japan. The ages of only two of these species are known with certainty: both are Miocene. All four species belong to the section CARPINUS, and were assigned to an organ genus, *Eucarpinoxylon*, by Müller-Stoll and Mädel.

Prakash *et al.* (1971) described two betulaceous woods from the Oligocene of Bohemia as species of the organ genus *Coryloxylon*. One species had features common to *Corylus* and *Ostryopsis*, the other features common to *Corylus* and section DISTEGOCARPINUS of *Carpinus*.

Fisk and DeBord (1974) report pollen of *Carpinus* from the strata containing the fossil forests in Yellowstone National Park, but there is no other record of the genus in the Eocene of the Rocky Mountains (Leopold & MacGinitie, 1972; MacGinitie, 1974). *Carpinus saximontana* represents the earliest known occurrence of wood with the structural features of the section CARPINUS and the first record of fossil wood of *Carpinus* in North America.

According to Willis (1973), *Carpinus* has 35 species which are north temperate (chiefly East Asian) in distribution, with only one species, a member of the section CARPINUS, indigenous to North America.

Carpinus absarokensis Wheeler, Scott, & Barghoorn, sp. nov.
FIGURES 6, 7.

Growth rings. Distinct, 3–5 mm. wide.

Vessel elements. Solitary, in radial multiples of 2–5, and less frequently in pore clusters; gradually decreasing in size through growth ring; tangential diameter of early wood vessels 51–97 μm., mean 74 μm.; tangential diameter of late wood vessels 32–60 μm., mean 46 μm.; in some growth rings the last portion of the late wood devoid of pores; length 635–850 μm.; perforations predominantly simple; intervascular pitting alternate to 10 μm. across; angular in outline where crowded; pits to ray parenchyma oval in outline.

Parenchyma. In longitudinal sections strands with up to 10 cells observed, apparently apotracheal diffuse distribution.

Rays. 1 to 3 (rarely 4) cells wide and aggregate; homocellular and occasionally heterocellular; multiseriate rays 5–39 cells, 94–740 μm. high; uniseriates 2–16 cells, 47–357 μm. high.

MATERIAL. One specimen of silicified, mature secondary xylem, 38 × 65 × 125 mm.

HOLOTYPE. U.S.G.S. Fossil Wood Collection No. D2054B-32. The species name indicates its occurrence in the Absaroka Volcanics.

LOCALITY. Specimen Ridge Fossil Forest: U.S.G.S. Paleobot. Loc. No. D2054B.

This species of *Carpinus* differs from *C. saximontana* in two features. Radial multiples are composed of no more than 5 vessels in *Carpinus absarokensis*, while in *C. saximontana* there are up to 14 pores per multiple. Some axial parenchyma cells in the Gallatin specimens are inflated and crystalliferous; no such cells were seen in *Carpinus absarokensis* from Specimen Ridge. These two species differ from one another in as many characters as do any other fossil wood species of *Carpinus* (see Müller-Stoll & Mädel (1959) for descriptions of the other species).

There is the possibility that the Gallatin woods and the wood from Specimen Ridge may represent but one species. Six specimens of *Carpinus caroliniana* Walter were examined. It was observed that the wider the growth ring, the more vessels the radial multiples at the end of the growth ring contained. The growth rings of the Specimen Ridge *Carpinus* are not as wide as those in the Gallatin woods. Five of the specimens of *C. caroliniana* Walter had inflated crystalliferous ray cells; one lacked such cells. Presence of crystalliferous cells varies within this one extant species. *Carpinus caroliniana* has a wide range and occurs in the eastern United States, Mexico, Guatemala, and Honduras. All but one of the specimens examined was from the eastern United States. The Mexican specimen was distinct in possessing abundant one-cell-wide bands of parenchyma. Variation in number of vessels per radial multiple and ray width were observed

in four other species in which more than one specimen was studied.

Although the differences between the Gallatin and Specimen Ridge woods assigned to *Carpinus* may be interspecific, they are named as separate species. There is interspecific variation in *Carpinus*, as evidenced by *C. caroliniana*, but wood of different species of *Carpinus* is in some cases more similar than *C. saximontana* and *C. absarokensis*. All three of the Gallatin specimens differ in the same features from the Specimen Ridge woods. For these reasons, the woods from the two localities are given different names.

LAURACEAE

Ulminium porosum Wheeler, Scott, & Barghoorn, sp. nov.

FIGURES 8–11.

Growth rings. Present, indistinct without magnification.

Vessel elements. Diffuse porous, solitary and oval, or in radial multiples of 2–5, mostly 2–3; tending to a diagonal arrangement; tangential diameter 40–115 μm., mean 92 μm.; radial diameter of solitary pores 75–185 μm., mean 120 μm.; 32–85 per square mm.; length 230–505 μm.; perforation plates simple; intervascular pitting alternate; medium-sized, angular in outline due to crowding; pitting to ray parenchyma variable, rounded, oval, or irregular, occasionally unilaterally compound, simple to slightly bordered; tyloses present.

Parenchyma. Difficult to distinguish in cross section; in tangential section strands observed in association with vessel elements.

Rays. Multiseriates to 5 cells wide, 8–56 cells, 140–1400 μm. high, with uniseriate margins of 1–3 rows of square and occasionally upright cells; uniseriates rare, to 7 cells high; inflated cells occasionally occurring in the marginal rows of the multiseriate rays.

Imperforate tracheary elements. Thin-walled, pitting not observed.

MATERIAL. Four specimens of mature, silicified, secondary xylem.

HOLOTYPE. U.S.G.S. Fossil Wood Collection No. D2054A-24, 40 × 50 × 73 mm. The specific name refers to the high vessel density.

LOCALITIES. Gallatin Fossil Forest: U.S.G.S. Paleobot. Loc. No. D2089. Amethyst Mountain: U.S.G.S. Paleobot. Loc. No. D2054A. (The holotype specimen is from Loc. No. D2054A.)

Four specimens have been placed in this taxon, two from the Gallatin fossil forest and two from Amethyst Mountain. They differ slightly in the density and tangential diameter of the vessels. According to Stern (1954) and Süss (1958), the presence of the following combination of features delimits the Lauraceae from other dicotyledonous families: a) diffuse porous wood; b) vessels predominantly solitary with a tendency

for the formation of short, radial multiples; c) crowded alternate intervascular pitting; d) heterocellular rays, mostly 1 to 3 cells wide; e) paratracheal vasicentric parenchyma; and f) presence of idioblasts. These Yellowstone specimens have a higher vessel density than is typical for the family (Metcalfe & Chalk, 1950; Stern, 1954), but because they have the distinctive combination of features listed above they are placed in the Lauraceae.

Unfortunately, *Ulminium* is the valid generic name for woods of the Lauraceae. Unger (1842) first used the name *Ulminium diluviale* for a fragment of wood which Felix (1883) re-examined and found to have abundant secretory cells and other characteristics of the Lauraceae. Page (1967) and Romero (1970) have discussed the validity of *Ulminium* for lauraceous fossil woods. In the past most fossil woods thought to belong to the Lauraceae have been assigned to *Laurinoxylon* Felix.

More recently, Page (1967) described *Ulminium pattersonensis* and *U. mulleri* from the Upper Cretaceous of California. These two species may represent the stem and root of the same lauraceous plant (Page, 1967). The pore multiples are 8-shaped rather than θ-shaped; the vessels are thick-walled and not arranged in diagonals.

Prakash, Brezinova, and Buzek (1971) and Prakash, Brezinova, and Awasthi (1974) have described two new Bohemian species of *Ulminium* (*Laurinoxylon*) and have listed the several European occurrences reported since Süss's (1958) monograph of fossil lauraceous woods.

It is impossible to correlate the species of *Ulminium* (*Laurinoxylon*) with modern species or even genera within the Lauraceae. We compared the wood of eight different specimens of *Cinnamomum camphorum* and found vessel diameter and density, parenchyma abundance, and frequency of oil cells to vary as much among these individuals as between different species of the same genus. Difficulties in distinguishing genera on the basis of wood anatomy have been discussed by Stern (1954) and others.

Leaves of *Cinnamomum*, *Cryptocarya*, *Litsea*, *Persea*, and *Sassafras* are reported from the late early Eocene of Wyoming (MacGinitie, 1969), and there are two species of *Laurophyllum* in the Kisinger Lakes flora (MacGinitie, 1974). The 32 genera of Lauraceae are primarily tropical and subtropical, with the chief centers of distribution for the family being in Southeast Asia and Brazil.

Laurinoxylon pulchrum Knowlton (Knowlton, 1899; Platen, 1908) and *Perseoxylon aromaticum* Felix (Felix, 1896; Knowlton, 1899) are two taxa of fossil woods from the Specimen Ridge area of Yellowstone Park which were assumed at the time they were described to belong in the Lauraceae. We have examined the type of *Laurinoxylon pulchrum* Knowlton and have found it to belong to the Leguminosae, rather than the Lauraceae. This wood will be discussed in detail in a subsequent paper. Süss (1958) suggested that *Laurinoxylon pulchrum* does not belong to the Lauraceae because there are no oil cells, and the vessel to parenchyma pitting was not described or illustrated by Knowlton. Platen (1908) described another specimen of this species; this specimen, from Amethyst Mountain,

is semi-ring porous and has small vessel to parenchyma pitting. *Sassafras* is the only lauraceous wood that is semi-ring porous, and small vessel to parenchyma pitting is not characteristic of the family. *Perseoxylon aromaticum* has larger vessels, a lower vessel density, no oil cells, and more parenchyma than *Ulminium porosum*. It is not possible to determine from the description and illustrations whether *P. aromaticum* was correctly assigned to the Lauraceae.

There are three types of fossil lauraceous woods from North America listed in Süss's (1958) monograph on fossil woods of the family. *Laurinoxylon bakeri* Berry from Texas has relatively abundant diffuse apotracheal parenchyma, as well as paratracheal parenchyma, low rays from 2 to 18 cells high, and some septate fibers. The diagnoses of *L. californicum* (Platen) Süss and *L. eberi* (Platen) Süss are unaccompanied by illustrations (Platen, 1908), and the descriptions are in such general terms that adequate comparison of these woods is impossible.

Ulminium parenchymatosum Wheeler, Scott, & Barghoorn, sp. nov.

FIGURES 12–14.

Growth rings. Indistinct.

Vessel elements. Tangential diameter 54–138 μm., mean 92 μm.; predominantly solitary (71%), in radial pairs (26%), and rarely in radial multiples of 3 (3%); multiples 8-shaped, rather than θ-shaped; walls 9.5–11 μm. thick; 5–8 per square mm.; length 285–430 μm.; perforations apparently all simple; intervascular pitting alternate, generally 8 μm. across; pits to parenchyma variable, not similar to intervascular pitting, often elongated horizontally, up to 14 μm. across; tyloses present.

Parenchyma. Vasicentric, aliform, and aliform-confluent.

Rays. Multiseriates to 4 cells wide; 7–42 (60) cells, 170–1035 μm. (1400 μm.) high; generally with a single marginal row of upright and square cells; occasionally with an inflated marginal cell; uniseriates 1–8 cells, 55–265 μm. high, some composed exclusively of upright and square cells; 4–8 per mm.

Idioblasts. Thin-walled cells, 15–35 per square mm.; as isolated cells or in small groups of 2–4; as single cells scattered among the fibrous elements, or to the side of a ray; 250–460 μm. long, tangential width 29–46 μm.

MATERIAL. One specimen of mature, silicified, secondary xylem 150 × 70 × 130 mm.

HOLOTYPE. U.S.G.S. Fossil Wood Collection No. D2054B-40.

LOCALITY. Specimen Ridge: U.S.G.S. Paleobot. Loc. No. D2054B.

This wood exhibits the combination of features listed previously as diagnostic of Lauraceae. It differs from *Ulminium porosum* and other species of fossil lauraceous wood by the presence of numerous idioblasts

scattered among the fibrous elements and of more abundant parenchyma.

Within the Lauraceae, idioblasts occur most commonly in ray or axial parenchyma cells, and less frequently in the fibrous ground tissue (Stern, 1954, and personal observation). Stern (1954) describes the idioblasts as "roughly barrel-shaped; that is vertically elongated and widest at the middle. These cells are distinguished from other similar cells by their non-lignified thin walls." The Yellowstone fossil described above has idioblasts which occur most frequently among the fibrous elements and only occasionally as marginal ray cells. In cross section, they are distinguished by thin walls and appear similar to idioblasts as figured by Stern (1954, *fig. 6*) and Jane (1970, *fig. 73C*). In tangential section the isolated cells are not as inflated tangentially as is figured by Stern (1954, *fig. 10*) or Jane (1970, *fig. 73B*) and do not appear barrel-shaped as is implied to be typical of these cells. Slides of the wood of 32 genera of Lauraceae (*fide* Kostermans) were examined to determine if idioblasts with a shape and distribution similar to the fossil existed. Cells with a similar shape to those in the fossil were found in some species of *Aiouea*, *Aniba*, *Beilschmiedia*, *Cinnamomum*, *Cryptocarya*, *Licaria*, *Litsea*, *Mezilaurus*, *Nectandra*, *Ocotea*, and *Phoebe*. The idioblasts were most frequently in ray and/or axial parenchyma, and isolated cells were mostly barrel-shaped. Idioblasts not markedly barrel-shaped and exclusively or predominantly in the ground tissue were observed in some species of *Aniba*, *Beilschmiedia*, and *Ocotea*. It is possible that these characters may occur in other genera. The presence or absence, distribution, and abundance of idioblasts may vary greatly within a genus. For example, in *Ocotea* there were species without any idioblasts, species where idioblasts occurred only in ray tissue, and others where idioblasts occurred only isolated among the fibrous elements.

As was discussed in relation to the species of *Ulminium* from Gallatin and Amethyst Mountain, in the Lauraceae there is as much variation within a genus as between genera; it is not possible to distinguish different genera, with the exception of ring-porous species of *Sassafras*. The species of *Ulminium* described above differs from previously diagnosed species of fossil lauraceous wood by the presence of numerous idioblasts among the fibrous elements and the relatively abundant parenchyma.

Ulminium eocenicum Wheeler, Scott, & Barghoorn, sp. nov.

FIGURES 15–17.

Growth rings. Indistinct.

Vessel elements. Tangential diameter 55–115 μm., mean 92 μm.; predominantly solitary (77%), occasionally in radial pairs (18%), and more rarely in radial multiples of 3 and clusters (5%); multiples 8-shaped, rather than θ-shaped; solitary vessels circular in outline, walls generally 10–11 μm. thick; 7–10 per square mm.; length 200–330 μm.; perforations simple; intervascular pitting alternate, small; pits to parenchyma variable, irregular in outline, at times unilaterally compound; occasional tyloses.

Parenchyma. Scanty paratracheal and vasicentric; also 3–8-cell-wide, widely spaced tangential bands.

Rays. Multiseriates to 4 cells wide; 6–30 (48) cells, 180–675 μm. (1105 μm.) high; generally with a single marginal row of square and upright cells, with up to 7 cells in the uniseriate margin; uniseriates 1–7 cells, 55–345 μm. high; 5–9 per mm.

Idioblasts. 1–2 per square mm., as isolated cells among the fibrous elements or adjacent to a ray, 220–295 μm. long, tangential width 23–32 μm.

MATERIAL. One specimen of mature, silicified secondary xylem measuring 100 × 72 × 85 mm.

HOLOTYPE. U.S.G.S. Fossil Wood Collection No. D2054B-38.

LOCALITY. Specimen Ridge: U.S.G.S. Paleobot. Loc. No. D2054B.

This species shares many features with *Ulminium parenchymatosum.* The salient features, which indicate that it is a member of the Lauraceae, are listed in the discussion of *Ulminium porosum. Ulminium eocenicum* is distniguished from *Ulminium parenchymatosum* by the smaller intervascular pitting, and the less abundant parenchyma and idioblasts.

MAGNOLIACEAE

Magnoliaceoxylon, gen. nov.

This is a genus for fossil woods belonging to the family Magnoliaceae but not assignable to an extant genus in the family. Structural features include most or all of the following: small vessels, solitary and in radial multiples, opposite and scalariform intervascular pitting, scalariform or in part simple perforation plates, and heterocellular rays usually not more than four cells wide with few uniseriates.

TYPE SPECIES: *M. wetmorei.*

The genus name *Magnolioxylon* was first used by Hofmann (1952) for a single species of Oligocene wood. No generic diagnosis was given, and her description of the type species, *M. michelioides*, does not include sufficient details to confirm its relationship either to *Michelia* or to the Magnoliaceae. Schönfeld (1958) and van der Burgh (1973) have indicated that the species does not correspond to *Michelia.* Since Kramer (1974b) mentions details not provided by Hofmann, he has apparently examined the type material. He records a combination of characters for *Magnolioxylon michelioides* that does not occur in the Magnoliaceae and concludes that the genus *Magnolioxylon* must be excluded from the family.

This nomenclatural situation, unfortunate but not unique, leaves no existing generic category for fossil magnoliaceous woods not assignable to extant genera. *Magnoliaceoxylon* is erected for such fossil woods.

Magnoliaceoxylon wetmorei Wheeler, Scott, & Barghoorn, gen. et sp. nov. FIGURES 18–20.

Growth rings. Present, indistinct.

Vessel elements. Predominantly solitary, or in radial multiples of 2–3; diffuse porous; tangential diameter 35–125 μm., mean 75 μm.; radial diameter solitary pores 55–135 μm.; 380–959 μm. long; perforation plates scalariform with 8–26 bars, most commonly less than 15 bars, bars occasionally forked; intervascular pitting opposite to scalariform; pit-pairs often with rectangular shape, squared at ends; pits to ray parenchyma scalariform, apertures larger than intervascular pitting.

Parenchyma. Not observed.

Rays. Multiseriates to 3 cells wide (very rarely 4 cells wide); 9–57 cells, 185–945 μm. high, uniseriate margins of 1–5 rows of upright and square cells, uniseriates rare, 3–10 cells, 85–290 μm. high, composed of square and upright cells; enlarged cells present in the uniseriate margins of the multiseriate rays; 5–9 per mm.

Imperforate tracheary elements. Nature not determinable, no pitting observed.

MATERIAL. One piece of mature secondary xylem measuring 115 × 95 × 70 mm.

HOLOTYPE. U.S.G.S. Wood Collection No. D2089-20. The species is named for Professor R. H. Wetmore, Harvard University, in recognition of his long and productive interest in plant anatomy.

LOCALITY. Gallatin Fossil Forest: U.S.G.S. Paleobot. Loc. No. D2089.

The combination of small vessels that are solitary and occasionally in radial multiples, scanty parenchyma, scalariform perforation plates, opposite and scalariform intervascular pitting, and inflated ray cells occurs in the Magnoliaceae. According to Metcalfe and Chalk (1950), enlarged oil cells in the margins of rays occur in *Talauma* and *Michelia*; additionally, Canright (1955) records their presence in *Aromadendron*, *Elmerillia*, and in the West Indian species of *Magnolia*. Record and Hess (1943) refer to oil cells as being associated with tropical members of the Magnoliaceae; species of temperate areas lack this feature.

Thin sections of the above five genera were compared with the fossil. *Michelia* differs in having a large number of radial multiples and perforation plates with less than six bars. *Aromadendron* has both simple and scalariform perforation plates. The fossil corresponds in some respects to *Elmerillia*, *Talauma*, and the West Indian species of *Magnolia* (*M. hamorii* and *M. splendens* examined). While most species of *Magnolia* have numerous, crowded vessels, predominantly in radial multiples, these West

Indian species do not. Neither *Elmerillia* nor *Magnolia* has as many bars per scalariform perforation plate as does the fossil. This may not be significant, in that fossil woods might be expected to have perforation plates with a larger number of bars (a more primitive feature) than do the modern taxa to which they are related.

It was not possible to determine definitely whether terminal parenchyma was present in this Yellowstone material. No parenchyma was observed with certainty in either transverse or longitudinal sections; however, as noted elsewhere (Scott & Barghoorn, 1955), it is often difficult to distinguish parenchyma in fossil wood. Some species of *Talauma* lack terminal parenchyma; it is present in *Magnolia* and *Elmerillia*. Canright (1955) characterizes *Talauma* as having apotracheal parenchyma, but it is not present in all species.

Despite the magnoliaceous characteristics of this fossil wood, it cannot be allied positively with a single modern genus in the family. Hence, it is described as the generitype of the organ genus *Magnoliaceoxylon*.

Kramer (1974b) has listed some of the fossil woods ascribed to the *Magnoliaceae*. In North America there are three reported occurrences: *Magnolioxylon panochensis* Page from the Upper Cretaceous of California (Page, 1970), *M. michelioides* Hofmann from the Oligocene of Saskatchewan, Canada, and *Talauma multiperforata* Kruse from the Eocene of Wyoming. Of these woods only *M. panochensis* appears to be assigned correctly to the Magnoliaceae. Accordingly, it is here transferred to become **Magnoliaceoxylon panochensis** (Page) Wheeler, Scott, & Barghoorn, comb. nov. (basionym: *Magnolioxylon panochensis* Page, Am. Jour. Bot. **57**: 1143. 1970).

Roy and Stewart (1970) described a specimen from the Oligocene of Canada which they considered to be conspecific with the *Magnolioxylon michelioides* described by Hofmann (1952). During re-examination of the Canadian material we found only crowded alternate intervascular pitting. Since such pitting does not occur in the Magnoliaceae, the Canadian wood is excluded from this family.

The type material of *Talauma multiperforata* (No. B-3283, Paleobotanical Collections, University of Cincinnati) was re-examined during this study. Kruse (1954) described the specimen as having scalariform, occasionally opposite, intervascular pitting and predominantly scalariform perforation plates. We found that the specimen had crowded alternate pitting, the pits being hexagonal due to crowding. The apertures were sometimes coalescent; perhaps this feature was mistaken for scalariform pitting by Kruse. Also, the majority of the perforation plates are simple rather than scalariform. This specimen is distinct from the Yellowstone *Magnoliaceoxylon*, which is characterized by opposite to scalariform intervascular pitting and exclusively scalariform perforation plates. Moreover, Kruse's specimen is not a *Talauma*. It does not belong in the Magnoliaceae, as alternate intervascular pitting does not occur in the family. Possibly, this fossil wood belongs in the Lauraceae, as is suggested by the presence of inflated secretory cells in the rays. This cannot be stated

with certainty, as neither parenchyma distribution nor vessel to ray parenchyma pitting could be observed.

There are three species assigned to *Magnolioxylon* from the Tertiary of Europe: *M. parenchymatosum* has small vessels, few bars per perforation plate, parenchyma in bands, and spiral thickenings in the vessels (van der Burgh, 1973); *M. krauselii* (Greguss) van der Burgh (1973) has smaller vessels, narrower rays, and some simple perforation plates; *M. scandens* has distinct growth rings, some simple perforation plates, and as many as 33 bars in the scalariform perforation plates (Schönfeld, 1958). Material of these species should be reviewed before possible reassignment to *Magnoliaceoxylon*.

Suzuki (1976) recently described *Michelia oleifera* from the Oligocene Tsuyazaki Formation of Japan. It differs from the Yellowstone wood in having numerous vessel multiples, a high (greater than 100 per sq. mm.) vessel density, and crystalliferous parenchyma cells.

No members of the Magnoliaceae are reported from the Kisinger Lakes flora (MacGinitie, 1974). *Magnolia* is among the genera in a preliminary list of late early Eocene megafossils from the Wind River Basin, Wyoming (MacGinitie, 1969). Magnoliaceous seeds from the late Paleocene of the Wind River Basin have been identified by Scott.

There are many temperate species in the Magnoliaceae, although others extend into the subtropics and tropics: *Elmerillia* contains seven species found in the Philippines and New Guinea; *Talauma* has 50 species now distributed in the eastern Himalayas, Southeast Asia, Malaysia, and from Mexico to tropical America (Willis, 1973).

PLATANACEAE [1]

Plataninium haydenii Felix, emend. Wheeler, Scott, & Barghoorn

FIGURES 21, 22.

Plataninium Haydeni Felix, Zeitschr. Geol. Gesell. **48**: 251. 1896.
Plataninium knowltoni Platen, Naturf. Gesell. Leipzig Sitzungsber. **34**: 130, 131. 1908.
Platanus haydeni (Felix) Beyer, Am. Midl. Nat. **51**: 564. 1954.

Growth rings. Present, narrow, marked by 2–3 rows of flattened fibers.

Vessel elements. Diffuse porous; predominantly solitary, in pairs, and with a tendency to formation of tangential arcs. Tangential diameter 41–

[1] After this paper had gone to press, a monograph by H. Süss and W. R. Müller-Stoll (Untersuchungen über fossile Platanenhölzer. Beiträge zu einer Monographie der Gattung *Platanoxylon* Andreánszky. Feddes Repert. **88**: 1–62. 1977) was received by E. W.

Süss and Müller-Stoll recognize four species of sycamore-like woods from Yellowstone: *Platanoxylon haydenii* (Felix) Süss & Müller-Stoll, *P. catenatum* Süss & Müller-Stoll, *P. knowltonii* (Platen) Süss & Müller-Stoll, and *P. platenii* Süss & Müller-Stoll.

92 μm. (mean 74 μm.); 44–108 per square mm.; length 460–900 μm.; perforation plates scalariform with 3–28 bars, most commonly with less than 10 bars; intervascular pitting opposite and subopposite, occasionally scalariform at tips; pits to parenchyma frequently elongate horizontally, scalariform.

Parenchyma. Apotracheal diffuse, as isolated cells and as short uniseriate bands.

Rays. To 22 cells wide and approximately 6 mm. high; uniseriates rare; wider rays either homocellular or heterocellular with 2–3 marginal rows of square and upright cells, narrower rays more commonly heterocellular.

Imperforate tracheary elements. Circular bordered pits mostly on the radial walls of the fibers.

MATERIAL. Seven specimens of mature, secondary xylem, D2054B-33, figured.

LOCALITIES. Gallatin Fossil Forest: U.S.G.S. Paleobot. Loc. No. D2089. Specimen Ridge: U.S.G.S. Paleobot. Loc. No. D2054B.

Of the seven specimens assigned to this taxon, four are from the Gallatin forest and three are from Specimen Ridge. They are representatives of a group of woods, common in the Eocene of western United States, that closely resemble modern *Platanus* (sycamore) woods but cannot reliably be assigned to this genus. The valid generic name for fossil woods of this structural type is *Plataninium* Unger, which has been emended recently by Page (1968) and by Brett (1972). Both Page and Brett emphasize the predominance of scalariform perforation plates in their generic concepts, and Brett, as did Vater (1884) in an earlier emendation, lists rarity of uniseriate rays as a diagnostic feature. This last feature is an important one in distinguishing sycamore woods from others with similar structure.

Page (1968) considered *Plataninium* to include fossil woods with the general structure found in *Platanus* (Platanaceae), *Fagus* (Fagaceae), *Euptelea* (Eupteleaceae), and *Citronella* and *Ottoschulzia* (Icacinaceae). All of these genera are characterized by numerous uniseriate rays together with the broad multiseriate rays. There are other distinctions between *Platanus* and these genera: *Euptelea* has perforation plates with many (up to 90) bars; *Citronella* and *Ottoschulzia* have markedly heterocellular rays and very long vessel elements (Page, 1968). Süss (1971) found height of procumbent ray cells to be another feature useful in distinguishing sycamore from structurally similar woods. The mean procumbent ray cell height in sycamore is 23–27 μm.; the ray cell height of the Gallatin and Specimen Ridge woods assigned to *Plataninium haydenii* falls within the range for *Platanus*.

In 1896 Felix described a sycamore-like wood from Yellowstone National Park as *Plataninium haydenii.* His diagnosis included these characters: distinct growth rings absent; rays noded at growth ring boundaries; vessels

extremely numerous, solitary and in pairs and irregular groups, diameter commonly 75–90 μm.; parenchyma in tangential bands, bands irregular and broken; rays 18–20 cells wide, some 1–2 cells wide; scalariform perforation plates and opposite intervascular pitting.

Later, Platen (1908) described an additional specimen of *Plataninium haydenii* and a new species, *P. knowltonii*, from Amethyst Mountain. The characters ascribed to *P. haydenii* are: distinct growth rings present; diffuse porous; vessels solitary and in tangential groups; vessel diameter generally 75 μm.; rays to 16 cells wide and to 5 mm. high. *Plataninium knowltonii* is diagnosed as having distinct growth rings, numerous vessels arranged in tangential rows, diameter of vessels up to 100 μm., intervascular pitting 5 μm. across, rays to 20 cells wide with uniseriate margins, and parenchyma in tangential bands. There do not appear to be significant differences between the diagnoses of *P. haydenii* and *P. knowltonii*, which we regard as a later synonym.

The likelihood that the Yellowstone sycamore-like woods represent a single taxon is borne out by the overlap in many features among the seven specimens of *Plataninium* that we have examined. A few examples do not show growth rings distinctly, but *P. haydenii* was described originally as lacking distinct growth rings. Among these specimens, the maximum number of bars per perforation plate varies from 10 to 41; the maximum vessel element length from 480 to 920 μm.; the maximum ray width from 16 to 26 cells. Uniseriate rays are rare. There is also variation in tangential diameter of vessels, vessel density, and abundance of parenchyma, but study of present-day sycamores indicates that such variations cannot be used to distinguish species. Süss and Müller-Stoll (1975) compared wood samples of five species of *Platanus* and concluded that size, density, and shape of the pores are not critical diagnostic features.

If these Yellowstone specimens of *Plataninium* were of different ages and were from diverse localities, they might be considered by some workers to represent distinct entities. However, they are of similar age and are in geographic proximity, and some of the specimens are intermediate in structure between the extremes listed above. We regard the specimens as exhibiting a reasonable range of variation for the single species, *P. haydenii*, as emended.

The major difference between *Plataninium* and extant sycamore wood seems to be the presence of exclusively or predominantly scalariform perforation plates in the fossil genus. This feature is mentioned in the original diagnosis of *P. haydenii*. However, Beyer (1954), who studied eight sycamore-like woods from Specimen Ridge, made the new combination *Platanus haydeni*. He describes these woods as having rays 3–10 cells wide and simple perforation plates. Nevertheless, he states (p. 565) that these specimens "conform so closely to *Plataninium haydeni* Felix that the deviations are only minute and fall well within a reasonable variation for the species." The differences in perforation plate type and ray width between Beyer's description and the original diagnosis of the species are not discussed.

The eight specimens cited by Beyer have been re-examined by courtesy of Dr. R. A. Davis, Department of Geology, University of Cincinnati. One specimen with relatively narrow rays (B-765), and another (B-779) that had wider rays more typical of Beyer's material, were sectioned. The rays had a maximum width of 16 cells in B-765 and 22 cells in B-779. Both specimens have exclusively scalariform perforation plates, the number of bars ranging from 3 to 31. It is difficult to reconcile Beyer's description with the actual anatomy of these woods. Because these specimens have exclusively scalariform perforation plates, there appears to be no justification for transferring them from *Plataninium* to *Platanus*.

Numerous occurrences of *Platanus*-like woods in the fossil record have been summarized by Prakash and Barghoorn (1961) and Prakash *et al.* (1971). In the last decade most forms with exclusively or predominantly scalariform perforation plates have been assigned to *Plataninium*; those with numerous simple perforation plates have been placed in *Platanus* or *Platanoxylon*, a name first used by Andreanszky (1951) and validated by Prakash *et al.* (1971). Two species of *Plataninium* are known from the Cretaceous of California (Page, 1968): *P. platanoides* has perforation plates with 4 to 22 bars; *P. californicum* has perforations with less than 30 bars and vessel elements longer than those found in modern *Platanus*. The Oligocene *P. europeanum* from Bohemia (Prakash *et al.*, 1971) has perforations with 13 to 30 bars. These authors have described a second sycamore-like wood from the same locality as a species of *Platanoxylon*; it is distinguished by numerous, although not predominantly, simple perforations. Both Bohemian woods show distinct growth rings. Page (1968) found a higher percentage of scalariform perforation plates in modern *Platanus* woods with indistinct growth rings as compared to those with distinct growth rings.

Sycamore-like woods are known from the Eocene London Clay Formation of England. *Plataninium decipiens* Brett (1972) has 13 to 25 bars per perforation plate, with some simple perforation plates present, especially in the early wood. In the same publication, Brett assigned another wood to *Platanus* sp. It is unclear why this specimen was called *Platanus* because it has exclusively scalariform perforation plates with 8 to 16 bars.

Fossil wood that seems truly to belong to *Platanus* has been described from Miocene sediments near Vantage, Washington, as *P. americana* Prakash & Barghoorn (1961). Simple perforation plates predominate in this wood. *Platanus* wood is also present in the Upper Miocene of Hungary (Süss, 1971) and the Oligocene of Japan (Suzuki, 1976).

A wide variety of fossil leaf types from the western United States has been assigned to the genus *Platanus*. MacGinitie (1974) points out that the genus apparently was undergoing complex genetic changes during Late Cretaceous and Paleogene time. This fact doubtless contributes to the reluctance of paleobotanists, including ourselves, to assign reasonably con-

vincing Eocene fossil woods to this extant genus, despite the fact that MacGinitie did recognize two species of *Platanus* from leaves in the Kisinger Lakes flora.

DISCUSSION

Recently, angiosperm paleobotanists have been reassessing the degree of relationship between early Tertiary and modern forms (Dilcher, 1973; Wolfe, 1973). It has been demonstrated that early Tertiary plants vary in their levels of similarity to extant plants. Some fossils are assignable to extant genera, others to families; still others cannot be reliably placed in any extant taxa. Most of the information on Paleogene plants comes from the study of leaves and pollen, rather than wood.

The eight species of Eocene fossil wood described here also show a variety of relationships to modern plants. *Alnus latissima*, *Carpinus saximontana*, and *C. absarokensis* have anatomy indistinguishable from extant members of these genera. The variable *Plataninium haydenii* has relationships with modern sycamores, but differs in having exclusively scalariform perforation plates, a feature that is more primitive. *Magnoliaceoxylon wetmorei* is a member of the Magnoliaceae, but its structural features do not seem equivalent to a single modern genus. The family Lauraceae has such homogeneous wood structure that comparison of the three species of *Ulminium* with modern genera is futile except to eliminate the ring porous species of *Sassafras*.

On the basis of eight species, it is not possible to venture more than the broadest paleoecological inferences. However, the general aspect presented by these eight plants is not dissimilar to that of larger Eocene floras. There is a mixture of so-called temperate and paratropical forms, as demonstrated by both by structure and by affinities with modern taxa. Some of the woods have well-defined growth rings with marked changes in vessel diameter and arrangement within a growth ring; the species of lauraceous wood, however, lack distinct growth rings, a characteristic not associated with temperate regions. However, it is possible that these detached pieces of wood may represent root wood, and growth rings are generally less defined in roots than in stems. Like tropical members of the Magnoliaceae, *Magnoliaceoxylon wetmorei* has inflated cells in the rays. Modern species of *Carpinus* and *Alnus* are predominantly temperate in distribution, and these Yellowstone species do not structurally resemble specimens from the southern hemisphere. *Alnus* pollen in tropical Eocene assemblages is thought to be transported from higher elevations (Germeraad *et al.*, 1968). Long distance transport of the Yellowstone woods is unlikely; it is thus possible that these Eocene species of *Alnus* and *Carpinus* may have had different ecological requirements than are now characteristic of the genera.

The early middle Eocene Kisinger Lakes flora from the nearby Wind River Basin is inferred to have grown under tropical or near tropical conditions with a pronounced winter dry season, and to have had a "distinct tropical American aspect" (MacGinitie, 1974, p. 1). This flora is con-

sidered to be distinct from older, early Eocene floras, whose primary relationships are with evergreen sclerophyllous broad-leaved and mixed mesophytic forest types, and which do not reflect the drier winter seasons of the middle Eocene. Although all of the fossil woods that can be assigned to extant taxa have New World relatives, they also represent plants which are present in either the evergreen sclerophyllous broad-leaved or the mixed mesophytic forest types. Thus far, the genus *Alnus* and the families Platanaceae and Lauraceae are common to the Kisinger Lakes flora and the Yellowstone fossil forest flora.

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EXPLANATION OF PLATES

PLATE I

FIGURES 1–3. *Alnus latissima*, sp. nov.: 1, transverse section, × 80; 2, perforation plate and opposite intervascular pitting, × 220; 3, tangential section showing aggregate ray, × 80. FIGURES 4, 5. *Carpinus saximontana*, sp. nov.: 4, transverse section, × 40; 5, tangential section showing aggregate ray, × 80. FIGURE 6. *Carpinus absarokensis*, sp. nov.: transverse section, × 70.

PLATE II

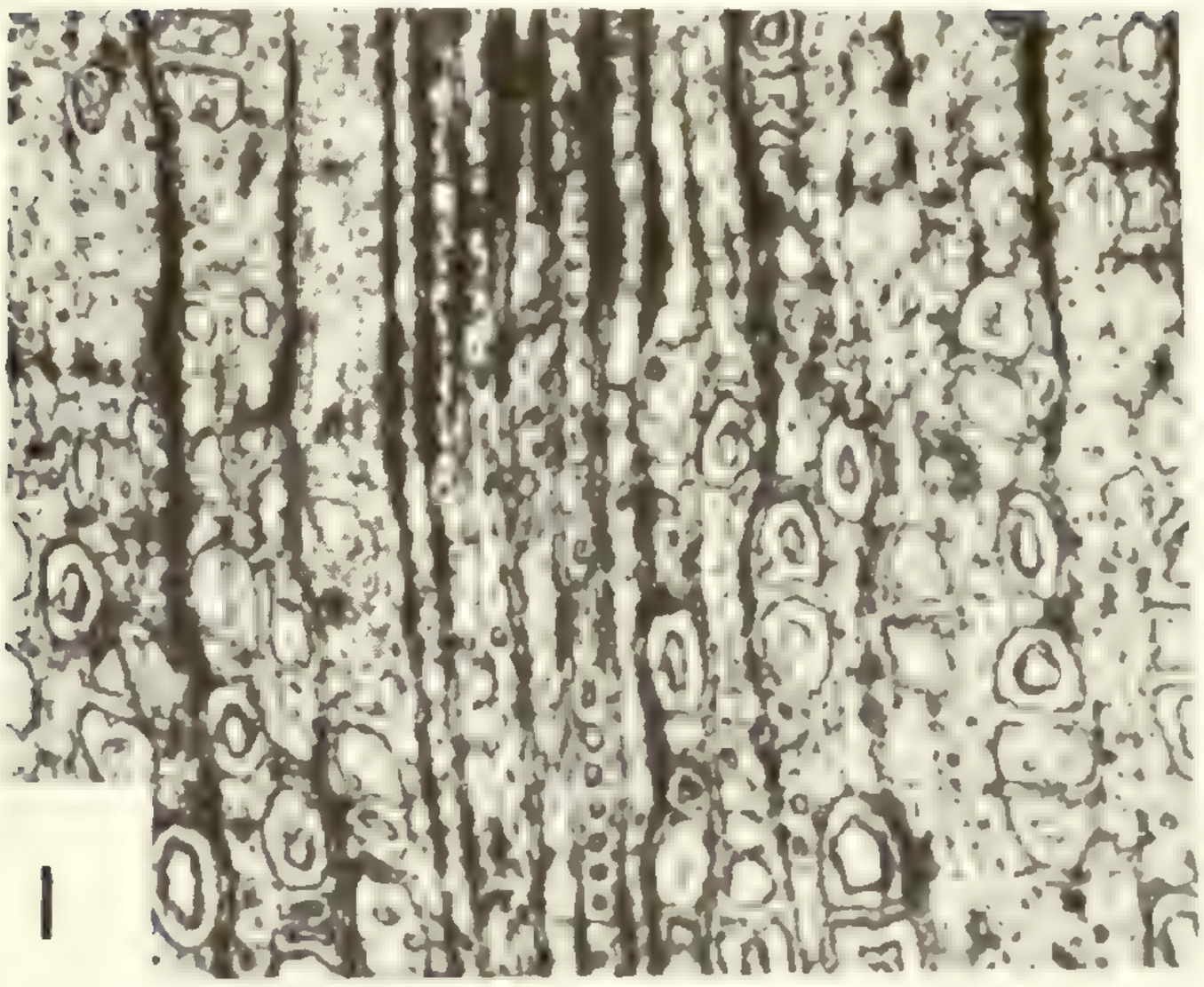
FIGURE 7. *Carpinus absarokensis*, sp. nov.: tangential section showing aggregate rays, × 80. FIGURES 8–11. *Ulminium porosum*, sp. nov.: 8, tangential section (note inflated ray cells), × 85; 9, transverse section, × 30; 10, intervascular pitting, × 250; 11, vessel to ray pitting, × 220. FIGURE 12. *Ulminium parenchymatosum*, sp. nov.: transverse section, × 45.

PLATE III

FIGURES 13, 14. *Ulminium parenchymatosum*, sp. nov.: 13, tangential section, intervascular pitting at left, idioblast at right, × 90; 14, vessel to ray pitting, × 200. FIGURES 15–17. *Ulminium eocenicum*, sp. nov.: 15, transverse section, × 55; 16, tangential section, idioblast at right, × 120; 17, intervascular pitting, × 200. FIGURE 18. *Magnoliaceoxylon wetmorei*, gen. et sp. nov.: transverse section, × 50.

PLATE IV

FIGURES 19, 20. *Magnoliaceoxylon wetmorei*, gen. et sp. nov.: 19, perforation plates and intervascular pitting, × 250; 20, tangential section, inflated ray cell at upper right, × 80. FIGURES 21, 22. *Plataninium haydenii* Felix emend.: 21, transverse section, × 65; 22, tangential section showing intervascular pitting and perforation plate, × 120.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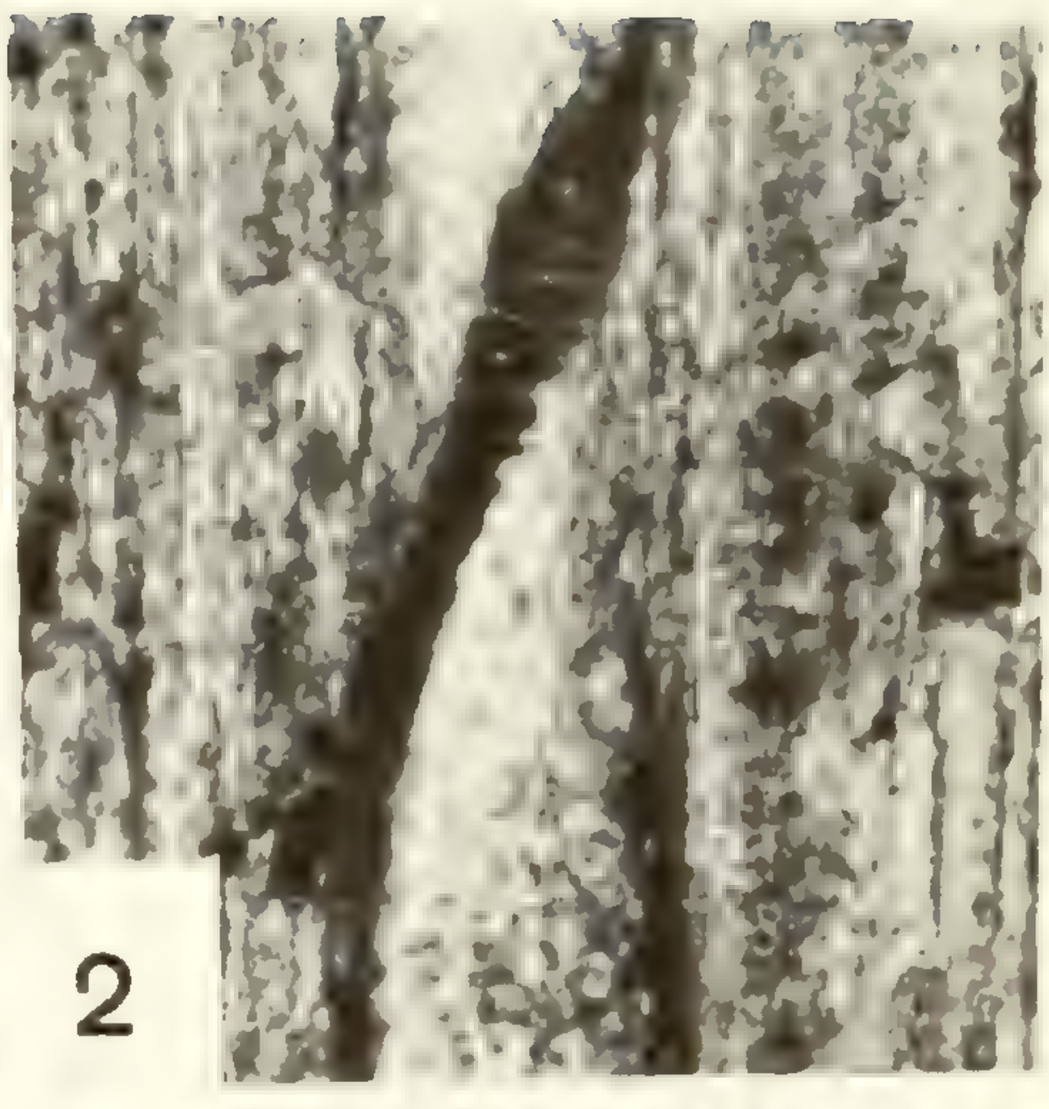
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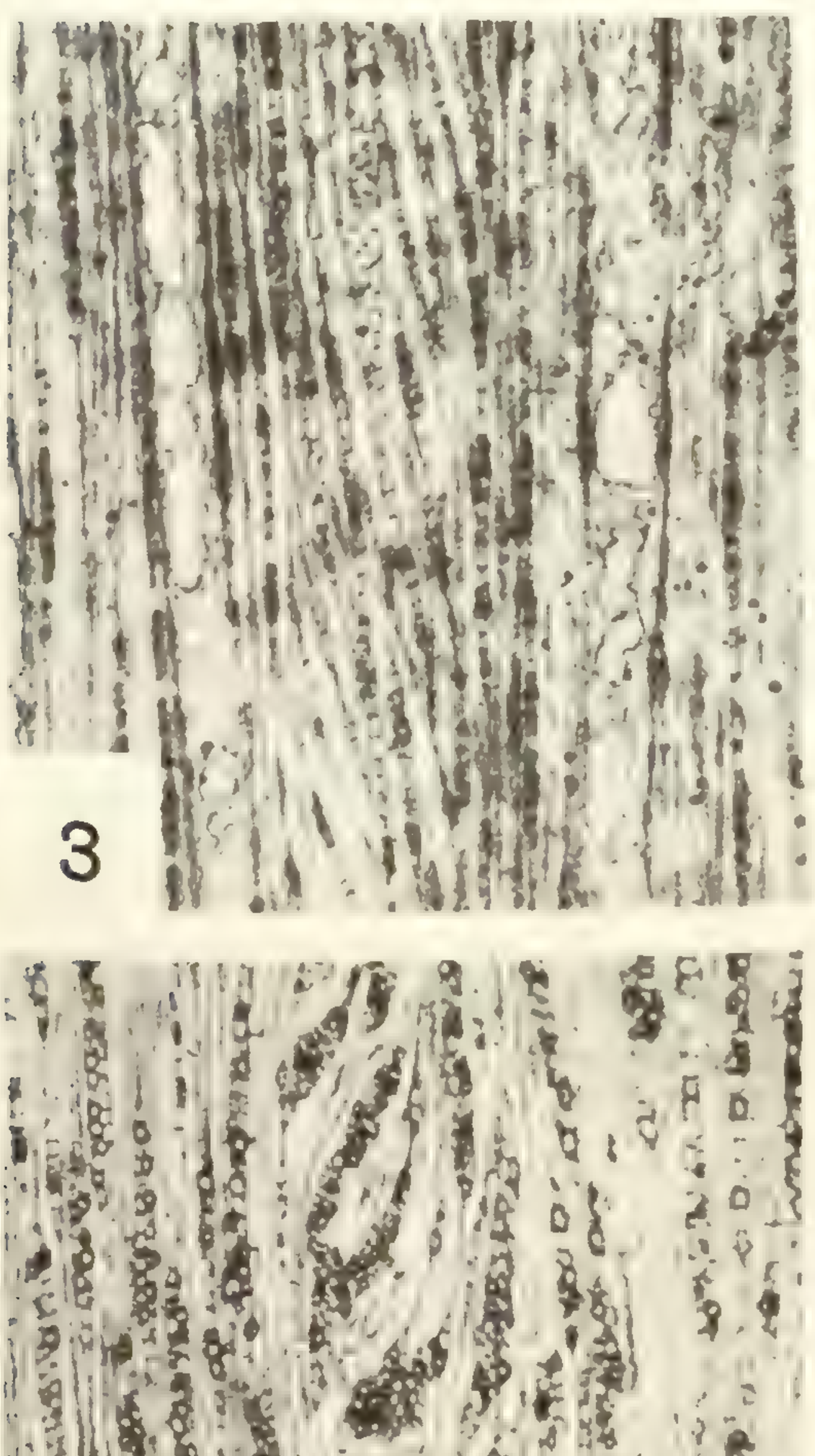
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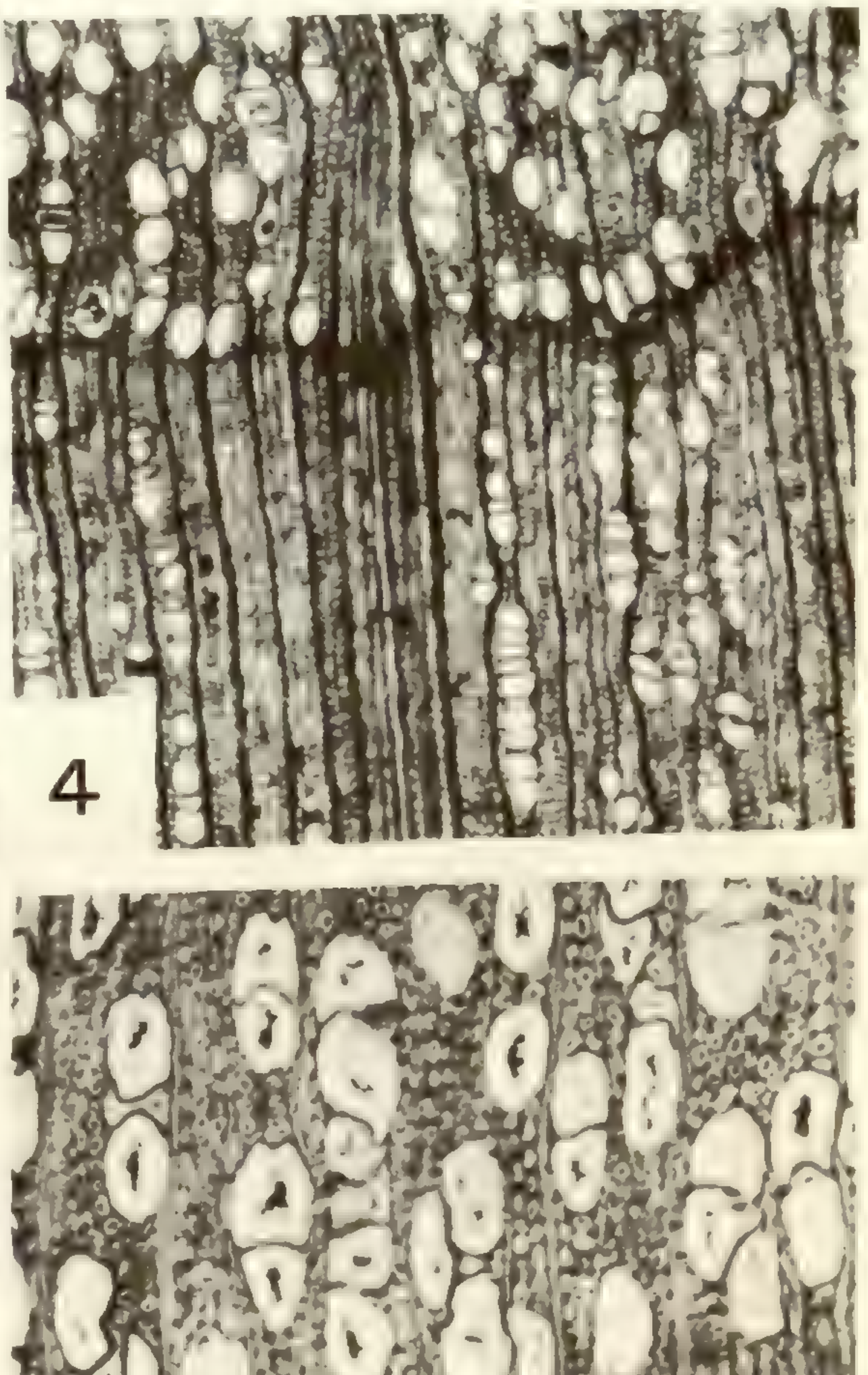
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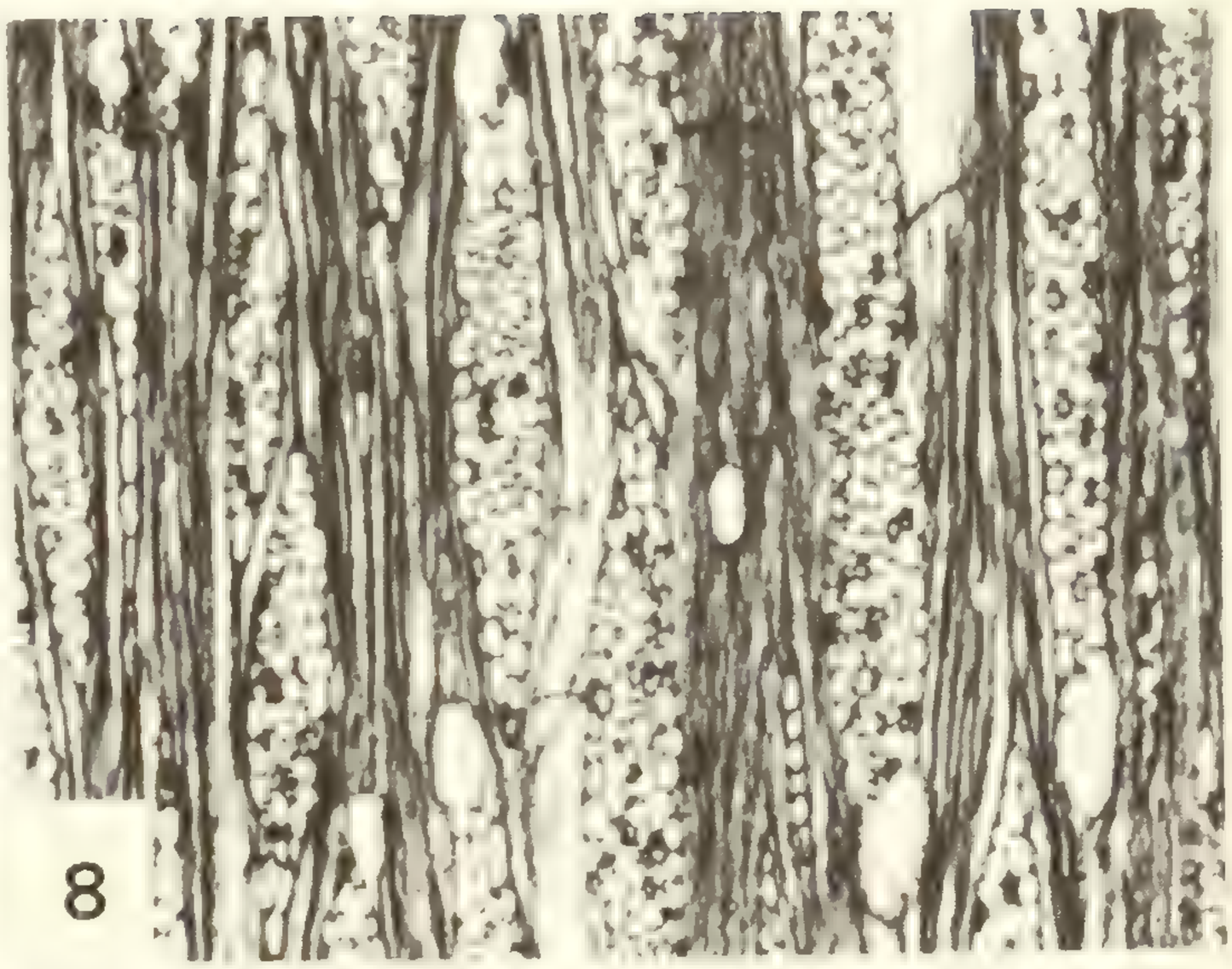
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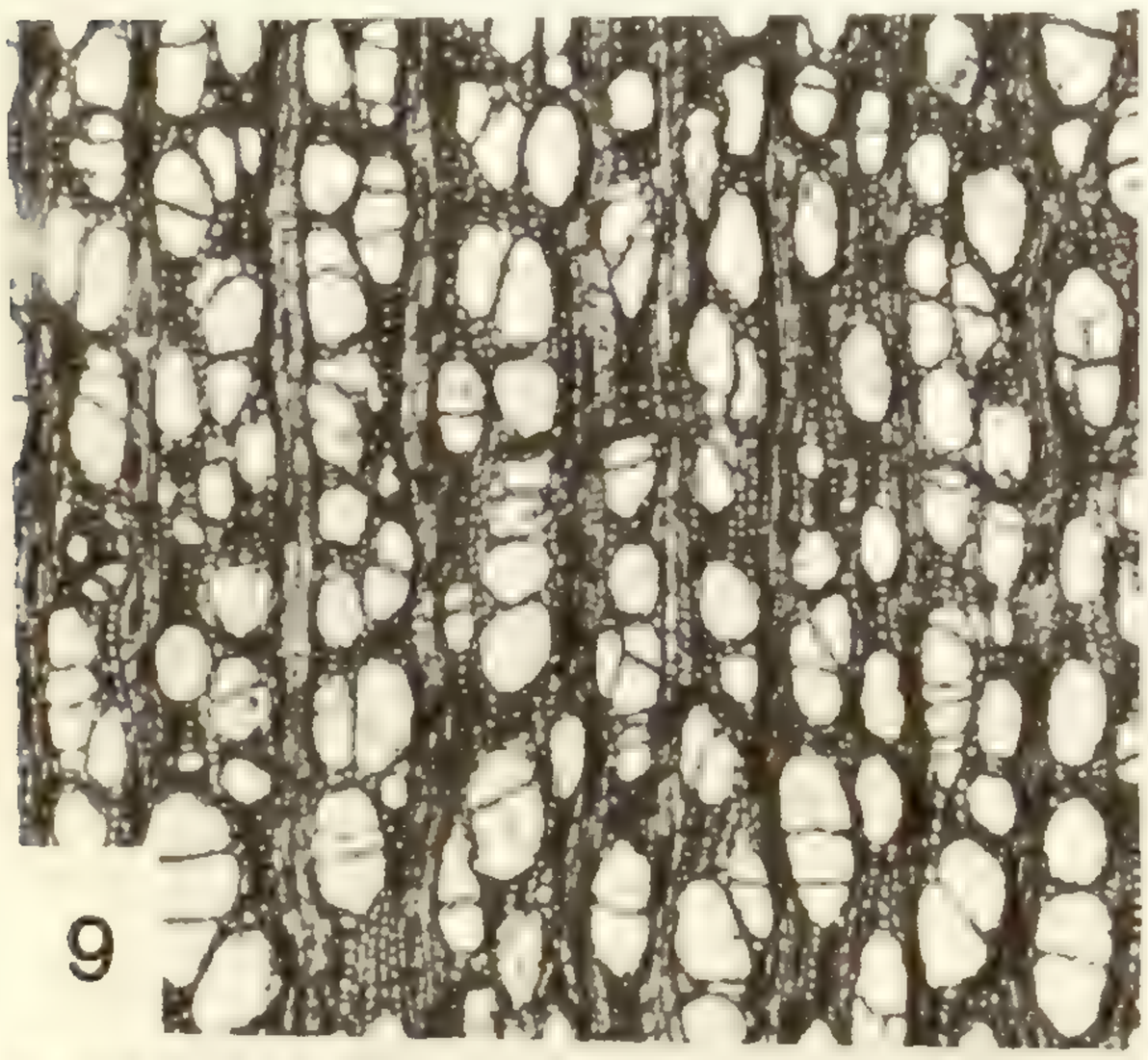
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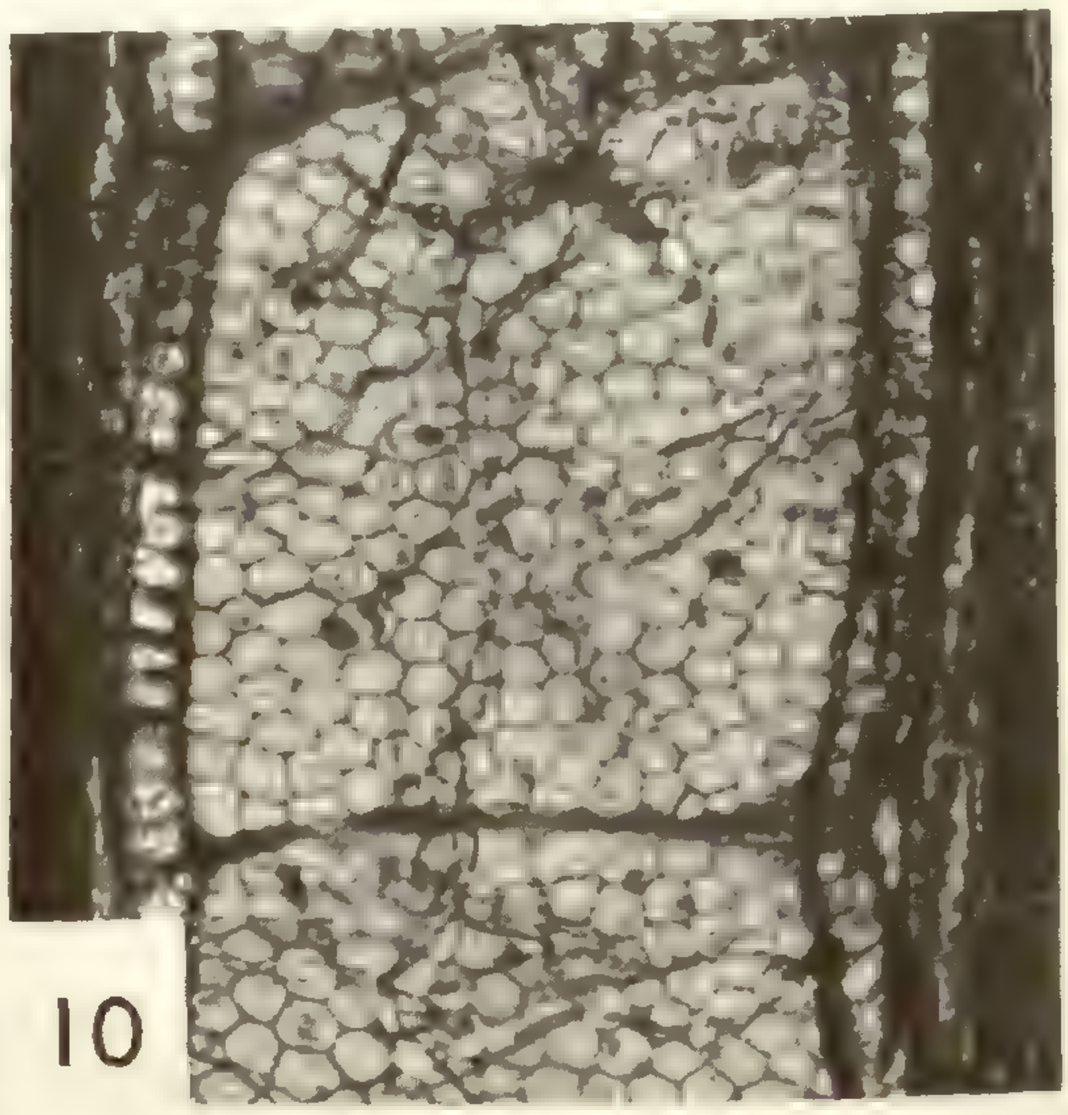
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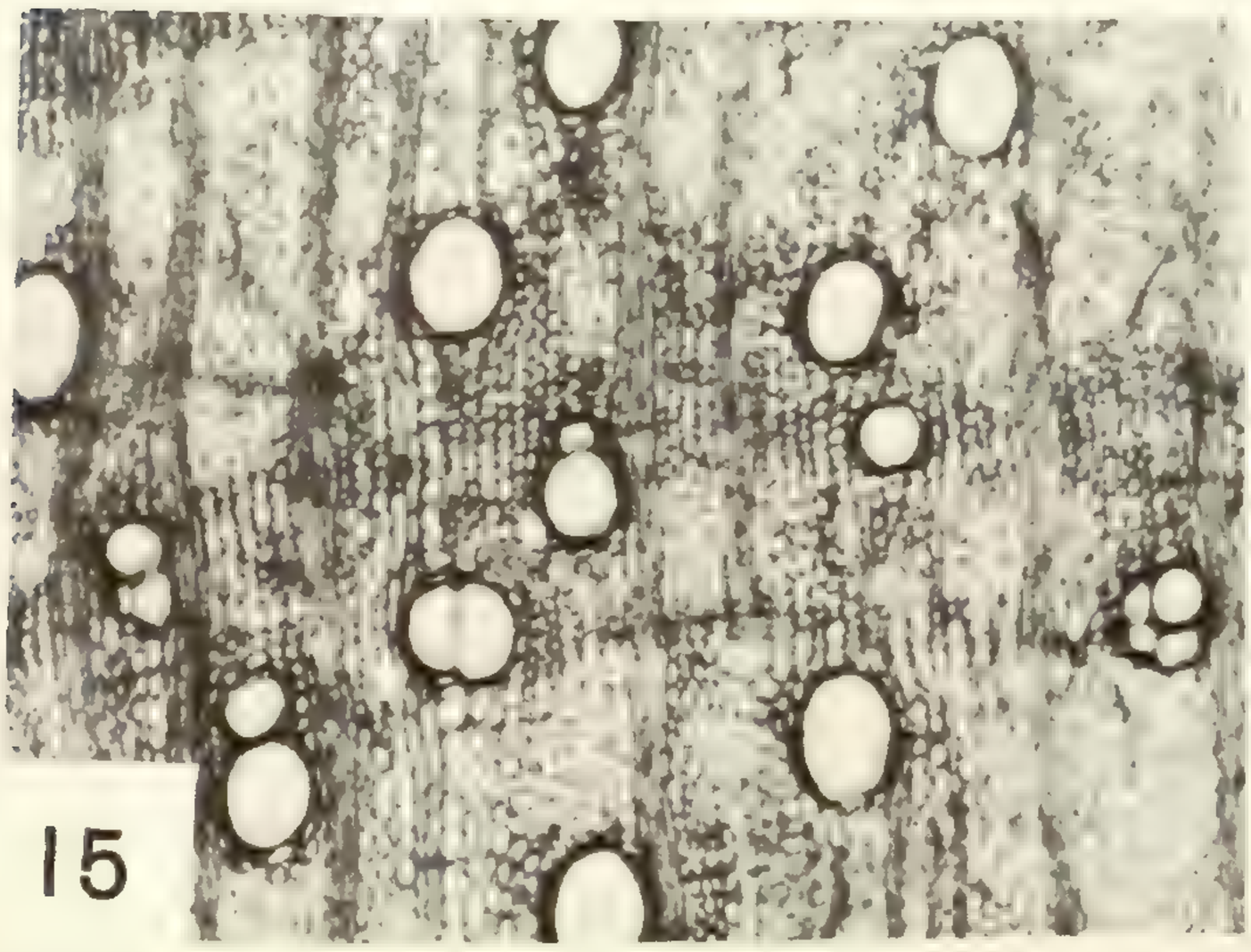

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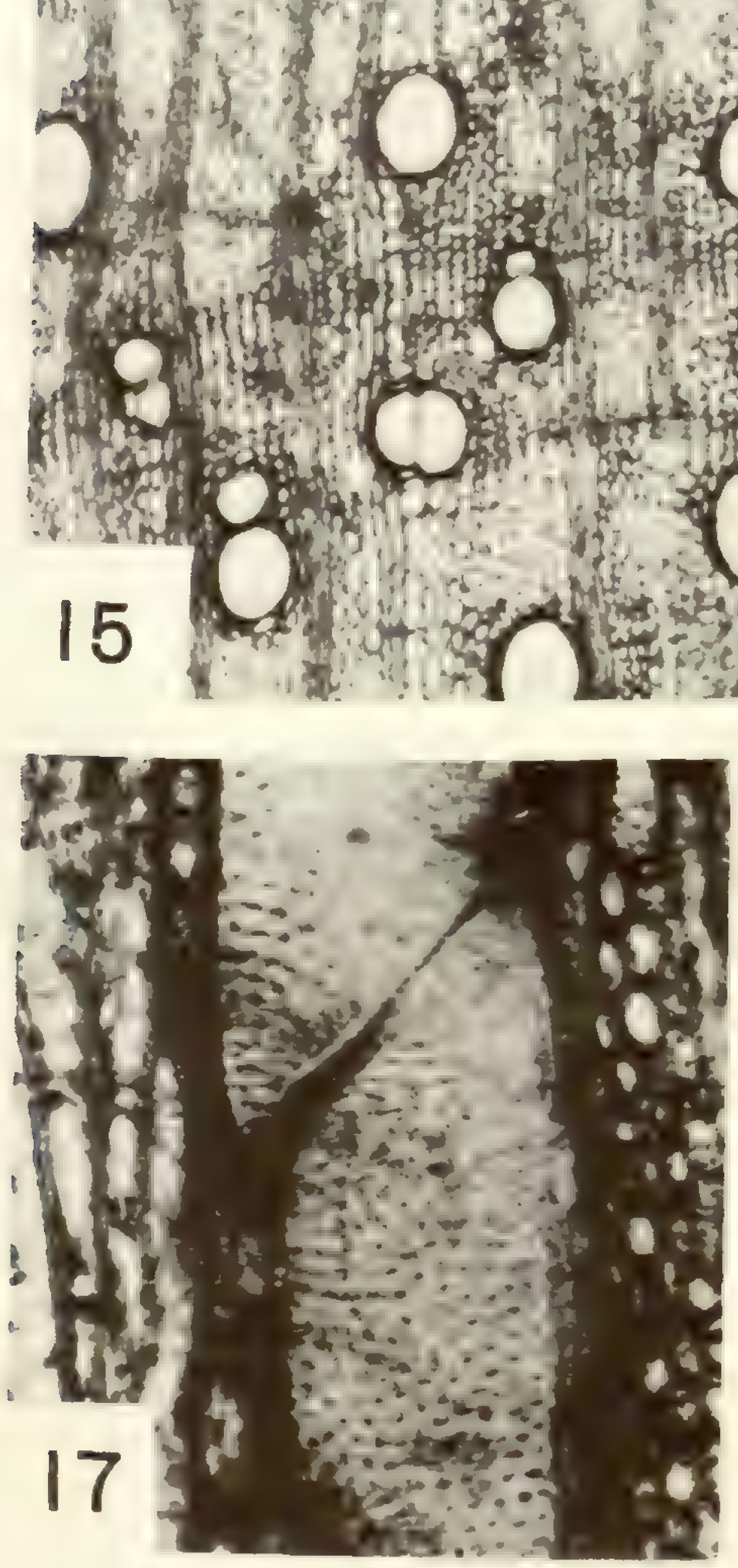

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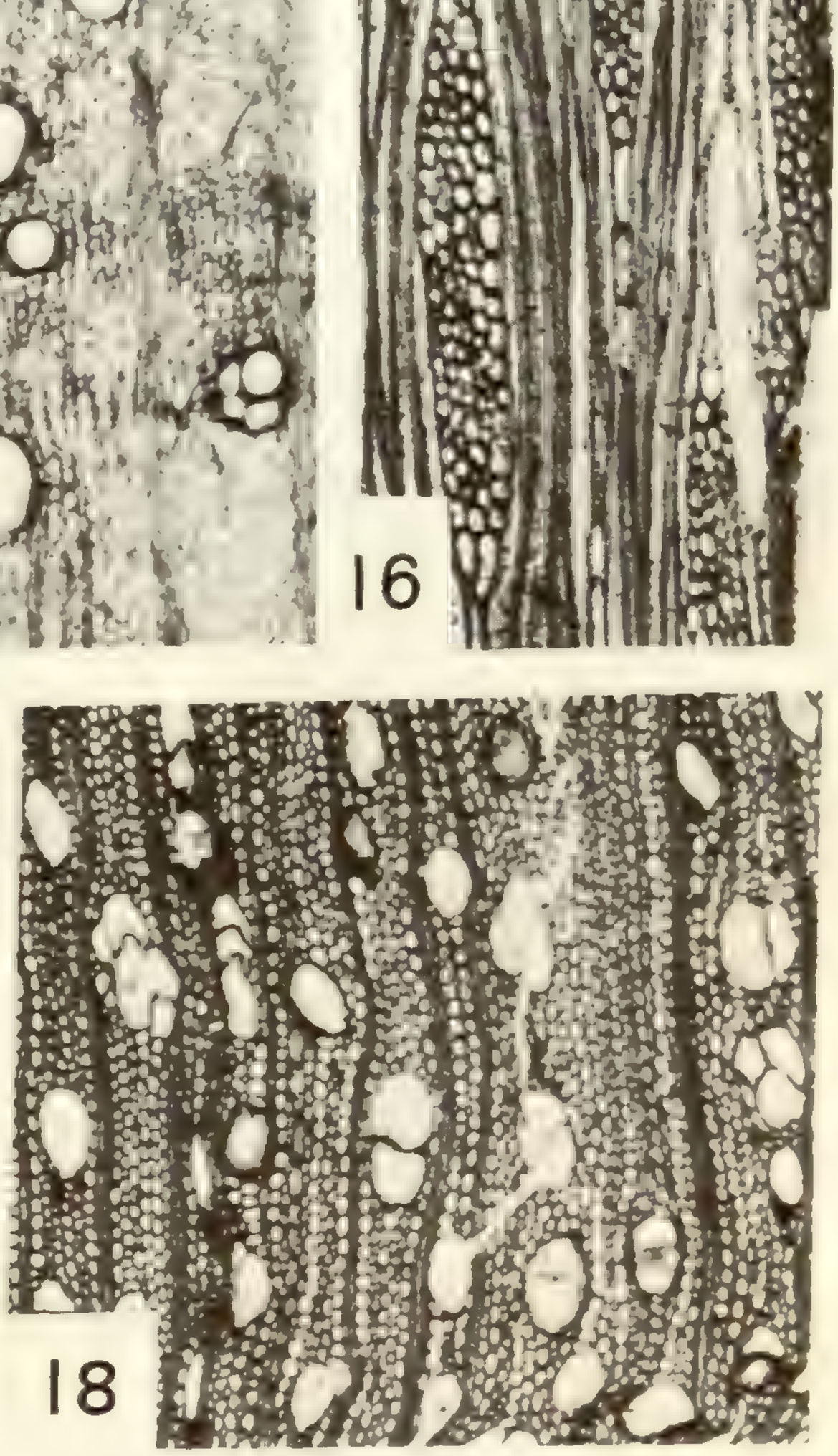

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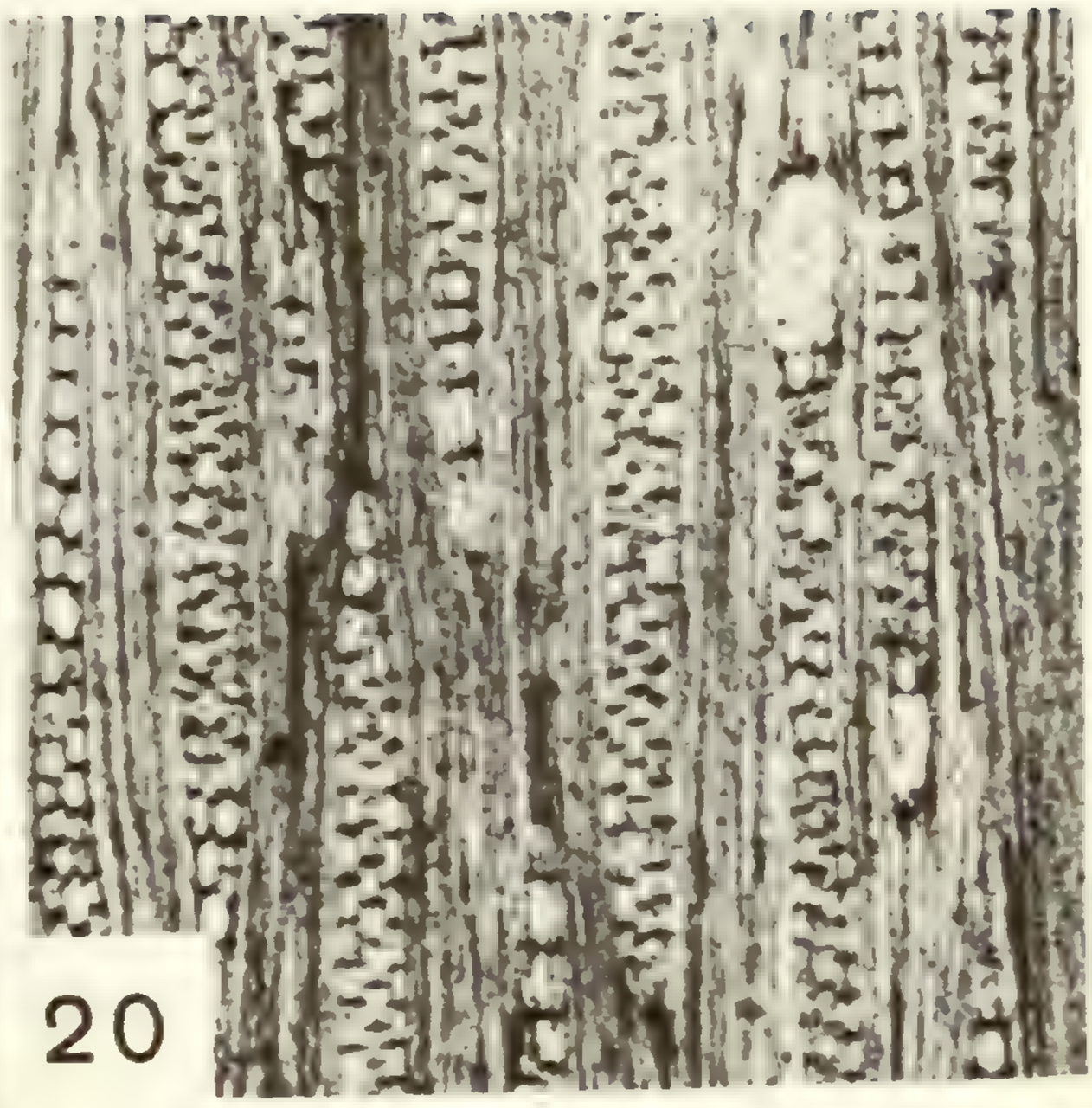
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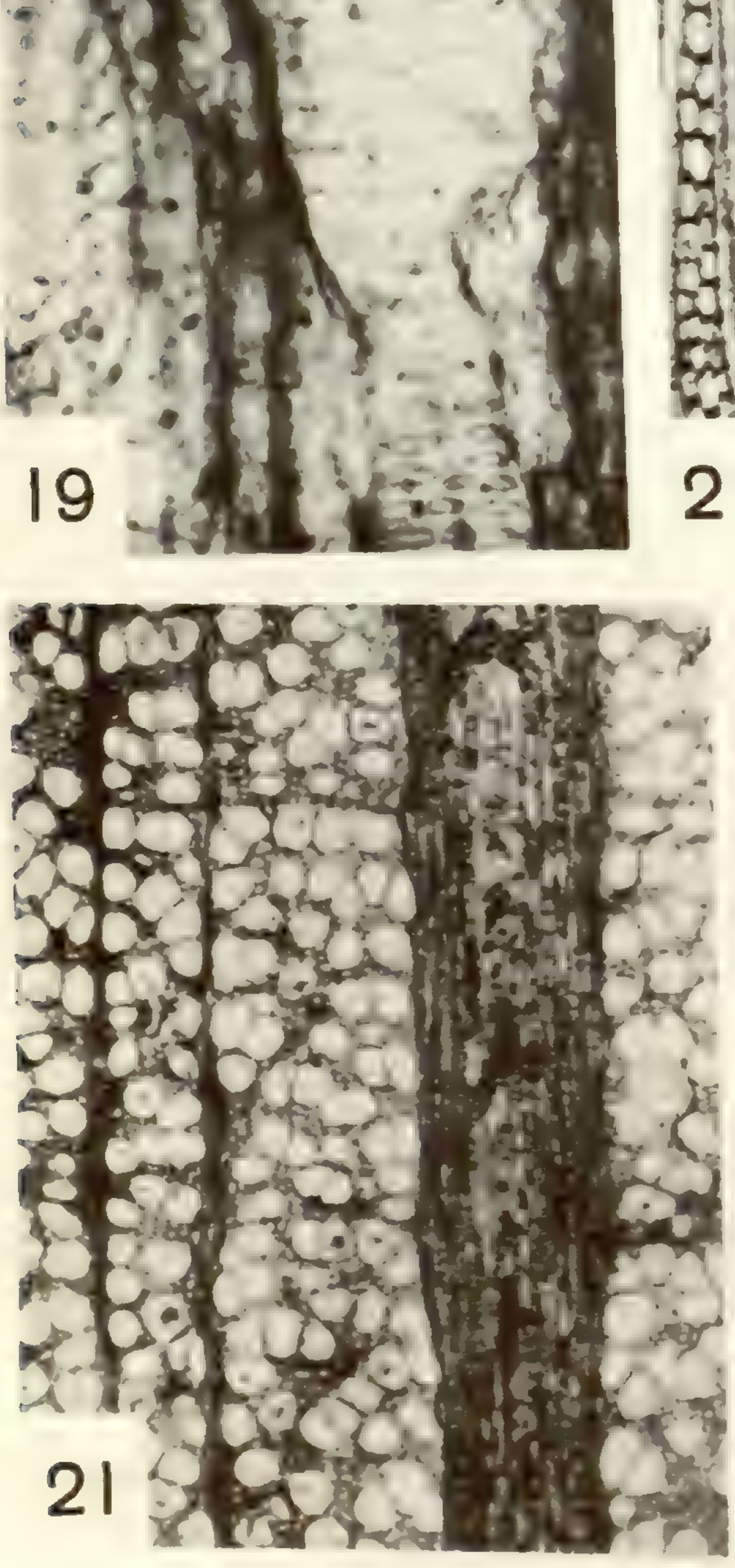
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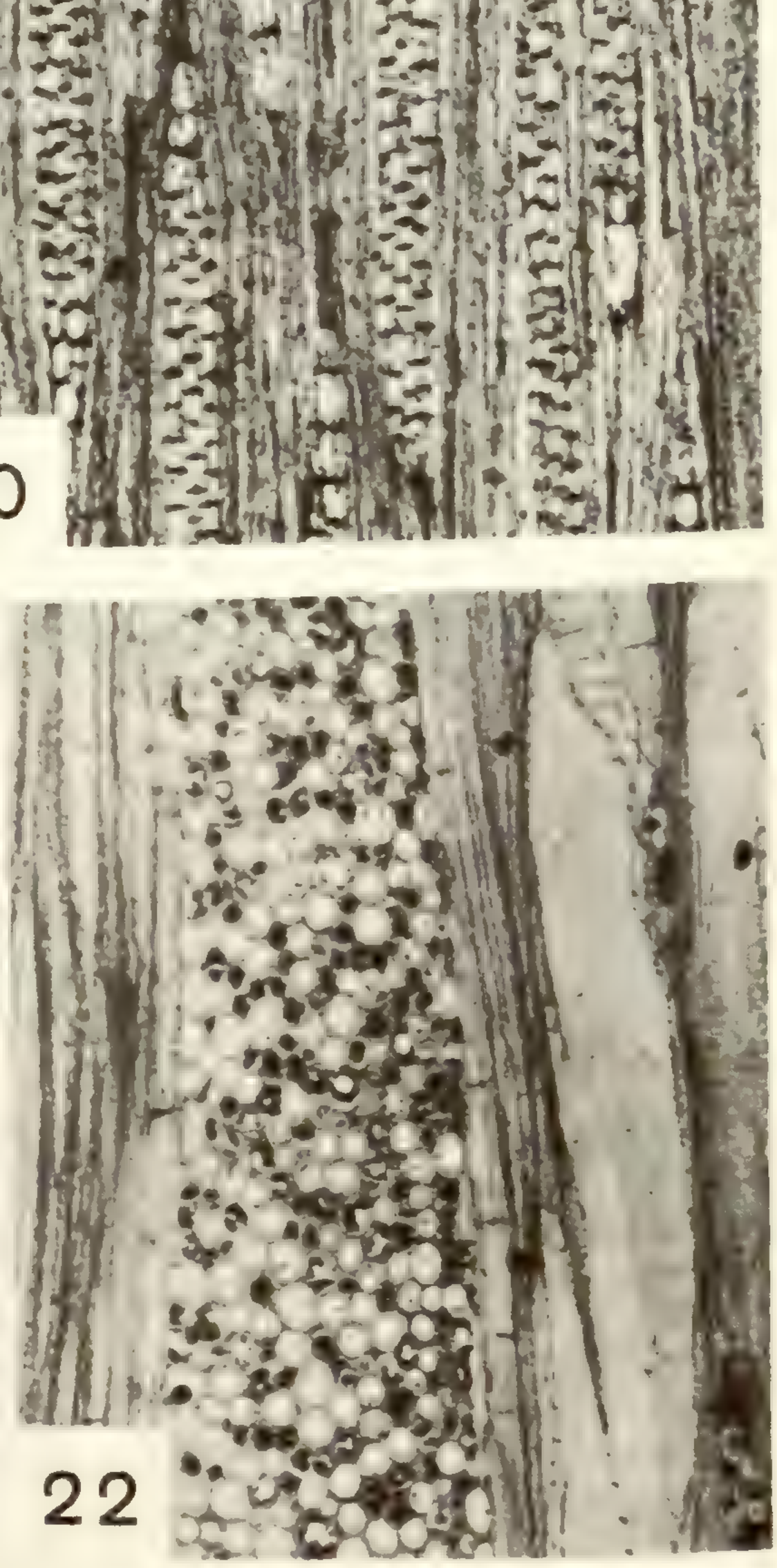
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SILVICAL CHARACTERISTICS OF SUGAR MAPLE, ACER SACCHARUM, IN NORTHERN CAPE BRETON ISLAND

K. N. H. GREENIDGE

A NUMBER OF FOREST TREE SPECIES of Canadian and Alleghanian affinity reach the limits of their natural ranges in northeastern Nova Scotia, failing to cross the Cabot Strait into nearby Newfoundland (Fernald, 1950; Rouleau, 1956; Little, 1971). Taxa reflecting this pattern of distribution include large-toothed aspen, *Populus grandidentata* Michaux; [1] ironwood, *Ostrya virginiana* (Miller) K. Koch; beech, *Fagus grandifolia* Ehrh.; red oak, *Quercus rubra* L. var. *borealis* (Michaux f.) Farw.; American elm, *Ulmus americana* L.; sugar maple, *Acer saccharum* Marsh.; white ash, *Fraxinus americana* L.; and hemlock, *Tsuga canadensis* (L.) Carr. In northernmost Cape Breton Island this complex of elements is marked by wide differences between species in abundance and local distribution. For example, hemlock, large-toothed aspen, and ironwood are occasional and are possibly restricted to a narrow range of sites (Roland & Smith, 1969). Oak demonstrates minor, localized discontinuities in range and fluctuates widely in abundance. Sugar maple is abundant and distributed over a very broad range of sites, manifesting considerable morphological variability.

Studies have been initiated to obtain detailed information on regional distribution patterns, local habitat preferences, and site-density relations in red oak, sugar maple, ironwood, and hemlock in northern Cape Breton Island. Preliminary information bearing on the distribution and abundance of sugar maple in this area has been published previously (Greenidge, 1972). The present paper includes observations on habitat preferences, site-density relations, and morphological variability in sugar maple, with emphasis on patterns evident in the Grande Anse, Aspy, and Northeast Margaree watersheds (FIGURE 1).

BEDROCK GEOLOGY, PHYSICAL GEOGRAPHY, AND SOILS

The primary physiographic feature of northern Cape Breton Island is a massive, geologically complex plateau comprising Precambrian schists, gneisses, quartzites, and crystalline limestones, intruded by granites of pre-Carboniferous age. Contiguous and included lowland areas, as well as the outlying lower hills flanking the plateau, are underlain by Carboniferous sedimentary rocks (Nova Scotia Department of Mines, 1965).

From the sea, or from a vantage point on the tableland, the surface of the plateau appears relatively flat. In actual fact, however, the elevation of this surface ranges from approximately 1000 feet (305 m.) in the south

[1] Nomenclature follows Fernald (1950).

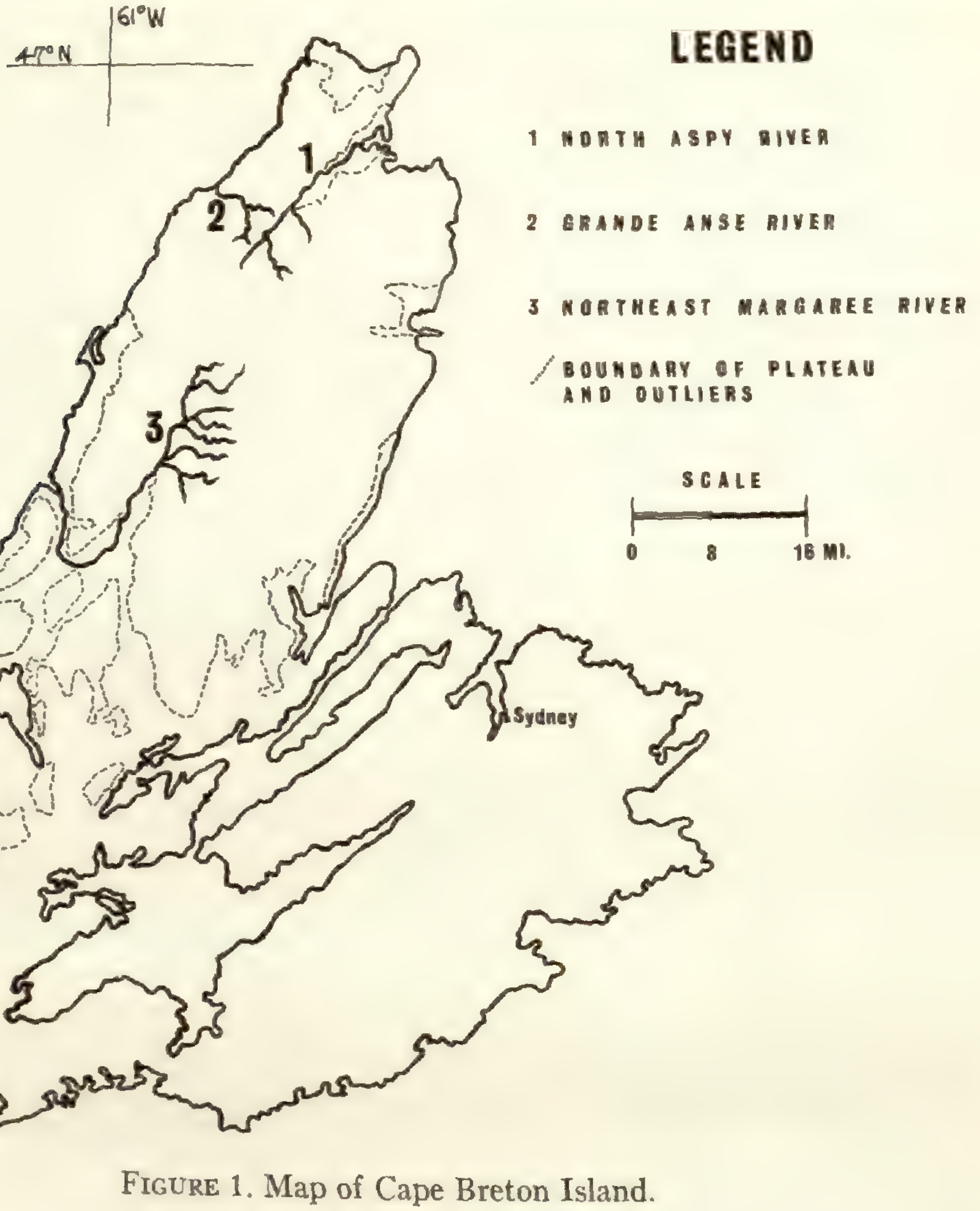

FIGURE 1. Map of Cape Breton Island.

to 1700 feet (518 m.) in the northern reaches of the island. Except to the southward, the flanks of the plateau either border the ocean or descend to a narrow coastal belt (FIGURE 1). There are strong indications of wide differences in the climate of upland versus lowland areas in northern Cape Breton. However, the absence of weather observation stations on the plateau surface renders valid quantitative comparisons impossible.

The tableland is being dissected by a number of short, swiftly flowing rivers and streams. Relief is considerable, and steep slopes form the approaches to the plateau, both from the sea and along the river courses. Instability is a common feature of many valley-side and seaward-facing slopes, and evidence of mass wasting is widespread. Slides and debris flows have occurred, and continue to occur frequently. In addition, accumulations of boulders, frequently of considerable extent, are common to many slopes.

Northern Cape Breton Island has been typed by Cann and MacDougall (1963) as rough mountain land characterized by steep slopes with ex-

cessively shallow, stony, weakly developed soils. The mapping of these soils was considered impractical by Cann and MacDougall. The bottomland soils of the sample areas have been mapped as deriving from fine-textured till, from medium-textured till with admixtures of alluvium, and from coarse-textured fluviatile materials.

PLEISTOCENE AND POST-PLEISTOCENE HISTORY

The glacial and postglacial history of northern Cape Breton Island is incompletely known. Evidence of extensive lowland glaciation has recently been reviewed by Grant (1971a; 1971b; 1972) and by Prest and Grant (1969). However, the surficial history of the upland surfaces remains obscure.

Prest and Grant (1969), while acknowledging the abundance of constructional glacial features in lowland Cape Breton, invite attention to the relative paucity of ice flow features on the highlands. Plateau surface configuration, together with the occurrence of areas of gruss and rotten rock resembling preglacial saprolite, led Newman (1971) to conclude that glacial erosion of the highlands was superficial. The filling and partial filling by till of deeply incised, V-shaped stream valleys, and the shallow depths of postglacial notching of bedrock-floored valleys have prompted Newman (1971) to suggest that the bedrock topography reflects a pre-Wisconsin, perhaps pre-Pleistocene landscape. However, Newman also presents evidence of topographic modification of pre-existing stream valleys, noting the presence of over-steepening in valley profiles, truncation of spurs, discordant stream junctures, and changes in valley form associated with changes in valley orientation.

Several sets of striae have been observed on the upland surface. Consistency in orientation of these striae has led Newman (1971) to conclude that northern Cape Breton was crossed by southeastward moving ice during the "classical" Wisconsin substage.

A rather different conception of the glacial history of the Cape Breton highlands has been developed by Prest and Grant (1969). In their view, the concept of Laurentide ice moving over the highlands is unacceptable. The available erosional and depositional evidence has prompted them to predicate the existence of a highland ice cap which was neither extensive nor active. In a later paper, Grant (1971b) developed this thesis further, interpreting crag and tail features on eastern and western slopes of the plateau as evidence of the existence of a "full-fledged" ice cap on the northern plateau.

In a more recent assessment, Grant (1975) presents a modified appreciation of his original thesis. A more complex sequence is envisaged, involving over-riding of the highlands by Laurentide Ice and subsequent occupation of the highlands and central plateau region by a local ice cap flowing radially to the sea. Age relations between Laurentide Ice and flow from the previously postulated lowland ice mass to the south have not been clarified (Grant, 1975).

On botanical and geological grounds, Fernald (1925) suggested that several upland surfaces (including the Cape Breton Plateau) in the Gulf of St. Lawrence region may have escaped glaciation. However, Livingstone and Estes (1967) conclude that the results of zoogeographic studies do not support "the botanical suggestion of a long, ice free history for the Cape Breton Plateau." Although Livingstone and Estes (1967) contend that appeal must be made to glaciation to explain the presence of numerous lakes on the plateau surface, they point out that the age of the lakes is unknown. Consequently, if formed early in the Wisconsin, the plateau surface might subsequently have served as a refugium for plants and animals.

Quaternary deposits bearing buried organic materials have been recognized and mapped in central and northern Cape Breton Island. Mott and Prest (1967) have discussed three such deposits, the ages of which range from >38,270 to >51,000 years. Deposition is thought to have occurred in preclassical Wisconsin time, and the deposits are related to an early Wisconsin interstadial interval. Newman (1971) has described a younger till with included organic materials which have been radiocarbon dated and accorded an age of the order of 21,000 years. Grant (1975) has reported four sub-till peat and wood occurrences from eastern Cape Breton Island which have been accorded ages of the order of 10,000 years. These deposits have been interpreted by Grant (1975) as indicative of a "significant readvance of the lowland ice mass ca. 10,000 years ago."

In the matter of deglaciation, Livingstone and Estes (1967) suggest that organic sedimentation on the Cape Breton Plateau was initiated about 9000 years ago. These authors postulate that prior to that time, an open tundra with scattered conifers and poplar characterized the upland surface, and that subsequent to the onset of organic sedimentation, a closed fir forest similar to the contemporary forests of parts of Nova Scotia has constituted the principal vegetation type. Prest's (1969) appreciation of the patterns of retreat of Wisconsin and recent ice indicates that the ice margin had reached the area of the Cape Breton Plateau about 12,500 years B.P.

FORESTS

The forests of northern Cape Breton Island have been discussed recently by Loucks (1962) and Rowe (1972). Consequently, only a brief, generalized description is included here.

Considerable variation in cover type is apparent in the forests of the sample areas. Bottomlands and lower slopes, together with the middle sections of stabilized, valley-side slopes, support virgin or disturbed, hardwood or mixed-wood forests differing widely in age, composition, and history. Stabilized, upper-valley-side slopes and the gentle, peripheral slopes of the plateau are characterized by a structurally variable, transitional forest comprising needle-leaved and broad-leaved elements in diverse mixtures

with a tendency toward regional differentiation. In the Aspy and Grande Anse watersheds, these upper-slope forests comprise mixed woods and mixed wood–softwood transitions, whereas in the Northeast Margaree the per centage of broad-leaved elements is higher.

On occasion, extensive areas of mid-slope and crest-slope segments of steep, valley-side slopes may support an irregular, unthrifty forest composed of white spruce, *Picea glauca* (Moench) Voss; and balsam fir, *Abies balsamea* (L.) Miller. Pronounced steepness, outcrops of bed rock, and a coarse, surficial mantle are commonly associated with this cover type.

The slightly rolling surface of the tableland supports a needle-leaved forest composed largely of balsam fir, with admixtures of white spruce; black spruce, *Picea mariana* (Miller) BSP.; larch, *Larix laricina* (Du Roi) K. Koch; and white birch, *Betula papyrifera* Marsh. The continuity of this plateau forest is broken by bogs and barrens of wide occurrence and considerable extent, by areas of wind-throw, and, in the south-central region, by recent clear-cutting operations.

METHODS

Field studies were concentrated in the lower and middle reaches of the North Aspy and Grande Anse rivers, and in the middle and upper Northeast Margaree (FIGURE 1). Sample plots were utilized to obtain information on occurrence and density on sites of limited topographic diversity, i.e., upland surfaces, terraces, and bottomlands. Conversely, distribution and density on topographically well-defined sites were investigated by means of cruise lines. Transects were disposed across contours on straight slopes in interfluve areas, and along the axes of spurs, stream-hollows, and valley-heads.

Morphological variation in sugar maple was investigated by means of stem-analysis trees and via diameter-height-age relations.

OBSERVATIONS

SITE-DENSITY RELATIONS

Bottomlands and foot-slopes. TABLE 1 includes data reflecting the occurrence and abundance of sugar maple in forested bottomland sites in northern Cape Breton Island. Valley-bottoms and foot-slopes [2] of the Grande Anse and North Aspy watersheds frequently support old-growth, broad-leaved forests in which the density (trees per acre) and basal area (sq. ft. per acre) of sugar maple are high, with the species represented over virtually the entire range of diameters encountered in the stands. The tolerance of sugar maple in these forests is expressed in its high percentage representation in the smaller diameter size classes, while its longevity and competitive potential are reflected in its continued high percentage occurrence in the middle and larger diameter size classes.

[2] Slope terminology follows Leopold, Wolman, & Miller (1964).

TABLE 1. **Diameter-density relations for sugar maple in old-growth, bottomland forests in northern Cape Breton Island.**

	GRANDE ANSE RIVER		NORTH ASPY RIVER		NORTHEAST MARGAREE RIVER	
	Number of trees		Number of trees		Number of trees	
DBH (in.)	All species	Sugar maple	All species	Sugar maple	All species	Sugar maple
4	39	22	63	19	73	24
5	20	18	34	9	44	23
6	15	12	25	8	25	9
7	22	15	22	6	21	16
8	19	15	25	10	23	19
9	16	12	18	10	15	12
10	15	13	17	10	18	16
11	11	9	14	7	14	14
12	15	12	13	5	15	14
13	17	13	13	8	9	9
14	9	3	12	9	5	3
15	12	9	9	5	19	17
16	8	5	9	4	10	9
17	11	9	7	6	4	4
18	9	2	5	3	6	5
19	8	5	7	6	5	5
20	7	3	3	3	2	1
21	8	3	7	4	5	4
22	3	1	2	—	4	2
23	2	1	2	1	2	2
24	5	1	5	3	2	2
25	—	—			1	1
26	3	—				
27	2	1				
28	4	—				
29	2	2			1	—
30	2	—				
31	3	—			1	1
32	2					
33	1					
34	1					
35	1					
36	—					
37	1					
38					1	—
Area (acres)	1.6		1.53		1.65	
Total trees	293	186	312	136	325	211
Trees per acre	183	116	204	89	197	128
Percentage	100	63	100	44	100	65
Basal area per acre	206 ft.²	88 ft.²	130 ft.²	73 ft.²	125 ft.²	97 ft.²
Percent	100	43	100	56	100	77

Despite proximity to the northeastern limits of the range of the species, individual sugar maples in these protected, bottomland stands reach impressive size and age. A large tree in the Grande Anse Valley, apparently felled in 1956, and displaying measurable diameter growth at the time of felling, was approximately 230 years of age at stump height. In a sample of six sugar maples measured in the Grande Anse Valley in 1967, diameters at breast height ranged from 14 to 34 inches (36–86 cm.), and heights, determined with the aid of an Abney level, varied from 79 to approximately 100 feet (24–30.5 m.). In the North Aspy and Northeast Margaree stands, canopy sugar maples vary from 75 to 95 feet in height (22.9–28.9 m.).

Canopy associates of sugar maple in old-growth, bottomland stands include yellow birch, *Betula lutea* Michaux f.; red maple, *Acer rubrum* L.; red oak; white ash, *Fraxinus americana* L.; white spruce, and balsam fir. Occasional balsam poplar, *Populus balsamifera* L., hemlock, and white birch occur in the canopy of the North Aspy stands.

With regard to regeneration, Clattenburg (1962) has estimated that in the Grande Anse stands, the number of woody plants per acre which exceed one foot (30 cm.) in height but are less than 3.5 inches (9 cm.) in diameter at breast height approximates 7915 stems. Included in this total are approximately 6000 sugar maple saplings. Clattenburg's estimate of the number of woody plants per acre under one foot in height is approximately 104,000, of which 94,000 are estimated to be sugar maple seedlings. Regeneration of sugar maple is less prolific in the North Aspy and Northeast Margaree stands.

Higher terraces and benches. The abundance of sugar maple on benches and terraces in northern Cape Breton Island varies widely. In undisturbed stands the species is commonly abundant on the treads of both strath and alluvial forms. However, very low densities of sugar maple are encountered in disturbed stands on the coarse-textured fans and fluviatile deposits of the Northeast Margaree River. Again, in a given reach characterized by the presence of two or more terrace levels developed in fluviatile materials, the density of sugar maple may be considerably higher on the lower or lowermost tread than at higher elevations. Density relations for sugar maple on strath and alluvial terraces are presented in TABLE 2.

It is clear that sugar maple may constitute a primary element of forests occupying both strath and alluvial terraces. In the North Aspy stands, the density and basal area of sugar maple approach levels characteristic of nearby bottomland forests. Individual sugar maples reach heights of 90 feet (27.4 m.) in these terrace forests, with the species distributed over virtually the entire range of diameters included in the plot tally. The diameter-class distribution of sugar maple suggests the continued primacy of the species on these surfaces. Canopy associates of sugar maple in the North Aspy terrace stands include red oak, red maple, yellow birch, and balsam fir. Regeneration of sugar maple is good in the North Aspy stands; it is not as good in the Northeast Margaree area.

TABLE 2. Diameter-density relations for sugar maple in undisturbed stands on strath and alluvial terraces.

	North Aspy River (strath)		Northeast Margaree River (alluvial)	
	Number of trees		Number of trees	
DBH (in.)	All species	Sugar maple	All species	Sugar maple
4	37	12	152	105
5	21	5	133	91
6	13	5	132	93
7	8	4	104	80
8	12	4	76	53
9	10	3	71	52
10	7	7	57	39
11	8	4	41	33
12	11	6	31	21
13	10	7	34	23
14	4	2	18	13
15	9	6	24	13
16	5	2	30	12
17	10	5	22	16
18	4	3	15	12
19	5	3	16	9
20	4	2	11	5
21	1	—	18	13
22	4	2	10	8
23	2	1	12	9
24	2	1	3	2
25	—	—	7	3
26	—	—	3	2
27	—	—	2	2
28	1	1	2	1
29			3	1
30			2	
31				
32			1	1
33			1	
40			1	
Area (acres)	1.2		6.2	
Total trees	188	85	1032	712
Trees per acre	157	71	166	115
Percentage	100	45	100	69
Basal area per acre	116 ft.^{2}	63 ft.^{2}	109 ft.^{2}	70 ft.^{2}
Percentage	100	54	100	64

Valley-side slopes and allied forms. Wide variations in density characterize the distribution of sugar maple on hill-slopes in northern Cape Breton. On straight slopes in interfluve areas, sugar maple varies in importance from a primary species to a minor element of the canopy. Well-defined differences in density are evident between slopes and between segments of the same slope within a modest altitudinal interval. TABLE 3 includes data reflecting abundance levels in sugar maple in transects extending from valley-bottoms to the plateau surface.

Reference to TABLE 3 indicates that in stream-hollows and valley-heads, where contours are disposed in a concave-outward pattern, the density of sugar maple is commonly high. Alternatively, on convex-outward forms (spurs), the density of the species reflects greater variability. On steep, narrow spurs lying between intersecting streams, the species frequently is virtually absent. However, on similar features of considerable lateral extent, bordered on either flank by subparallel drainage channels, the density of sugar maple occasionally may be moderately high (TABLE 3).

Data on variability in density of sugar maple with change in topographic setting, taken from a previous paper (Greenidge, 1972), are shown in TABLE 3. A transect was oriented parallel to but slightly downslope from the axis of a steep, narrow spur, across a shoulder, then into a stream-hollow crossing this feature diagonally. Emerging from the hollow, the traverse passed upward across a short, steep, straight slope, then on to the gentle peripheral slopes of the plateau surface.

The data indicate that sugar maple is absent to infrequent on the axis of the spur. The species increases in abundance on approaching the shoulder, and reaches maximum density in the stream-hollow. Beyond the stream-hollow the density of the species again decreases on the steep valley-side slope, declining steadily toward the plateau surface.

Plateau-surface. In the middle and upper reaches of the Northeast Margaree, the break in slope separating the steep valley-sides from the gentle approaches to the upland surface occurs at elevations of the order of 1100 to 1200 feet (335–366 m.) above sea level. This alteration in slope is commonly accompanied by striking changes in forest form and composition. Immediately above the break in slope, but below the elevation limit of the range of sugar maple (ca. 1300 feet (396 m.) in the Margaree watershed), the gently rising upland surface supports an open, parklike, mixed-wood forest composed of short-stemmed individuals of very poor form. Species represented in the canopy of these stands include yellow birch, white birch, sugar maple, red maple, balsam fir, and white spruce. In these virtually undisturbed, peripheral, upland forests, the percentage of sugar maple in the overstory may be moderately high, with the species occurring over a considerable segment of the range of diameters represented (TABLE 4).

TABLE 3. Diameter-density relations in sugar maple on valley-side slopes and allied topographic forms.

WATERSHED LOCATION	MARGAREE		GRAND ANSE		ASPY		ASPY		MARGAREE		MARGAREE			
Topographic setting	Valley-side slope		Valley-side slope		Valley-side slope		Broad spur		Stream hollow		Variable			
Density	**Trees per 0.1 acre**		**Trees per 0.1 acre**		**Trees per 0.1 acre**		**Trees per 0.1 acre**		**Trees per 0.1 acre**		Land form	**Trees per 0.1 acre**		
	All species	Sugar maple	All species	Sugar maple	All species	Sugar maple	All species	Sugar maple	All species	Sugar maple		All species	Sugar maple	
Distance plot center from datum (chains)														
1	35	12	12	8	28	2	36	5	38	22	Spur	29	4	
3	42	11	18	12	31	3	47	7						
5	39	10	18	14	30	1	22	10	48	34	Spur	23	0	
7	56	9	18	18	30	1	16	5						
9	49	8	16	16	38	0	21	6	32	26	Spur	21	0	
11	51	11	8	8	47	2	18	7						
13	58	5	24	16	46	0	22	12	36	23	Spur	23	3	
15	22	6	20	10	50	0	27	4						
17	23	1	12	6	(Outcrop)		25	5	33	3	Spur	28	0	
19	48	5	20	16	32	8	22	8						
21	42	8	18	16	18	5	34	7	24	17	Spur	39	3	
23	44	4	18	8	13	6	17	9						
25	54	8	24	6	21	18	19	17	20	18	Spur	47	0	
27	34	7	18	2	22	22	16	14						
29	23	15	22	0	20	7	12	9	37	6	Shoulder	34	3	
31	15	7	50	0	37	0	12	3						
33	16	0	12	0	20	0	21	3	46	—	Stream hollow	23	4	
35	35	0	40	0	32	0	14	1			"	18	11	
37			18	0			23	0						
39							27	0			Straight slope	37	3	
41														
43											Upland surface	11	1	
45														
47											Upland surface	35	0	
49														
51														

TABLE 4. **Diameter-density relations for sugar maple on the plateau surface.**

DBH (in.)	PERIPHERY OF PLATEAU SURFACE Number of trees		NEAR LIMIT OF RANGE Number of trees	
	All species	Sugar maple	All species	Sugar maple
4	113	84	44	3
5	74	49	21	3
6	74	52	30	5
7	41	31	21	6
8	62	45	12	1
9	57	47	22	5
10	54	42	15	4
11	43	35	21	4
12	35	25	16	3
13	17	13	4	0
14	20	15	9	0
15	19	10	7	2
16	8	7	4	0
17	5	1	4	0
18	4	2	2	1
19	6	0	1	0
20	2	0	3	0
21	—	—	5	0
22	2	0	—	—
23	2	0	1	0
24	2	1	4	0
25	1	0	—	—
26			2	0
27				
28				
29	1			
30	1			
31	1			
Area (acres)	2.4		1.1	
Total trees	644	459	248	37
Trees per acre	268	191	225	34
Percentage	100	71	100	15

However, as one approaches the altitudinal limit of the range of sugar maple in the Northeast Margaree region, the parklike quality of the upland stands becomes less evident, and there is a pronounced decrease in the density of sugar maple with a concomitant increase in the percentage of balsam fir. The actual "farthest-on" position of sugar maple comprises a zone of diffusely scattered trees. On the apparent limit of the range of the species, individual sugar maple stems show no evidence of depauperate habit, occurring rather as codominant members of the overstory, albeit of very poor form.

In the Grande Anse and North Aspy rivers, the break in slope separating

TABLE 5. **Diameter-height relations in sugar maple on a uniform site (valley-side and hollow of a small stream) over a 700-foot vertical interval.**

APPROX. ELEVATION (FT.)	DBH (IN.)	HEIGHT (FT.)
300	5	47
	7	64
	13	81
442	9	72
	12	74
537	7	56
	8	60
631	7	55
	9	57
	11	73
726	9	48
	11	57
820	8	45
	9	34
915	9	36
	12	41
1010	6	31
	11	33

the upland surface from the steep, valley-side slopes occurs at elevations of the order of 1350 to 1400 feet (412–427 m.). Sugar maple commonly attains the altitudinal limits of its range on the valley-side slopes and is not a frequent constituent of the plateau surface forests of these regions.

MORPHOLOGICAL VARIABILITY

Well-defined differences in height growth and form distinguish sugar maples on upland from bottomland sites in northern Cape Breton Island. As noted previously, sugar maples growing in the valley-bottoms of the Margaree and other streams may approach 100 feet (30.5 m.) in height. In contrast, on nearby upland sites some 1000 feet (305 m.) higher in elevation, sugar maples of considerable age (125 years and older) attain heights of 45 feet (13.7 m.) and less. Height-diameter relations for sugar maple on a relatively uniform site (valley-side and hollow of a small stream) extending over a 700-foot (213 m.) interval in the Margaree region are illustrated in TABLE 5.

Differences in the absolute size of trees from upland as opposed to bottomland sites are accompanied by equally well-marked differences in overall form. Codominant sugar maple stems in the diameter range of 7 to 11 inches (18–28 cm.) at breast height growing on good sites (i.e., protected, moist bottomlands) reach heights of the order of 60 to 80

feet (18.3–24.4 m.). Under these circumstances, length of bole per inch diameter at breast height ranges from 8.6 feet (2.6 m.) in the smaller (7 inch) size classes to 7.3 feet (2.2 m.) in the larger diameters. However, codominant trees within the same diameter range situated on crest slopes and the plateau surface fall between 35 feet (10.7 m.) and 50 feet (15.2 m.) in height. Thus, for codominant trees of equal diameter, length of bole per inch diameter at breast height in stems from protected bottomlands is approximately 60 percent greater than in material from the plateau surface. In terms of height and height-diameter relations, codominant sugar maples in protected valley-bottoms are taller and of considerably better form than individuals of the same diameter growing on upland sites. Patterns of height growth for codominant sugar maples located respectively on a protected lower slope, on an exposed mid-slope, and on the plateau surface are illustrated in FIGURE 2.

DISCUSSION AND SUMMARY

The landscape of northern Cape Breton Island is marked by considerable physiographic diversity. Topographic variability, together with differences in surficial geology and land surface history, contributes to the existence of a wide spectrum of habitats available to plants. As indicated

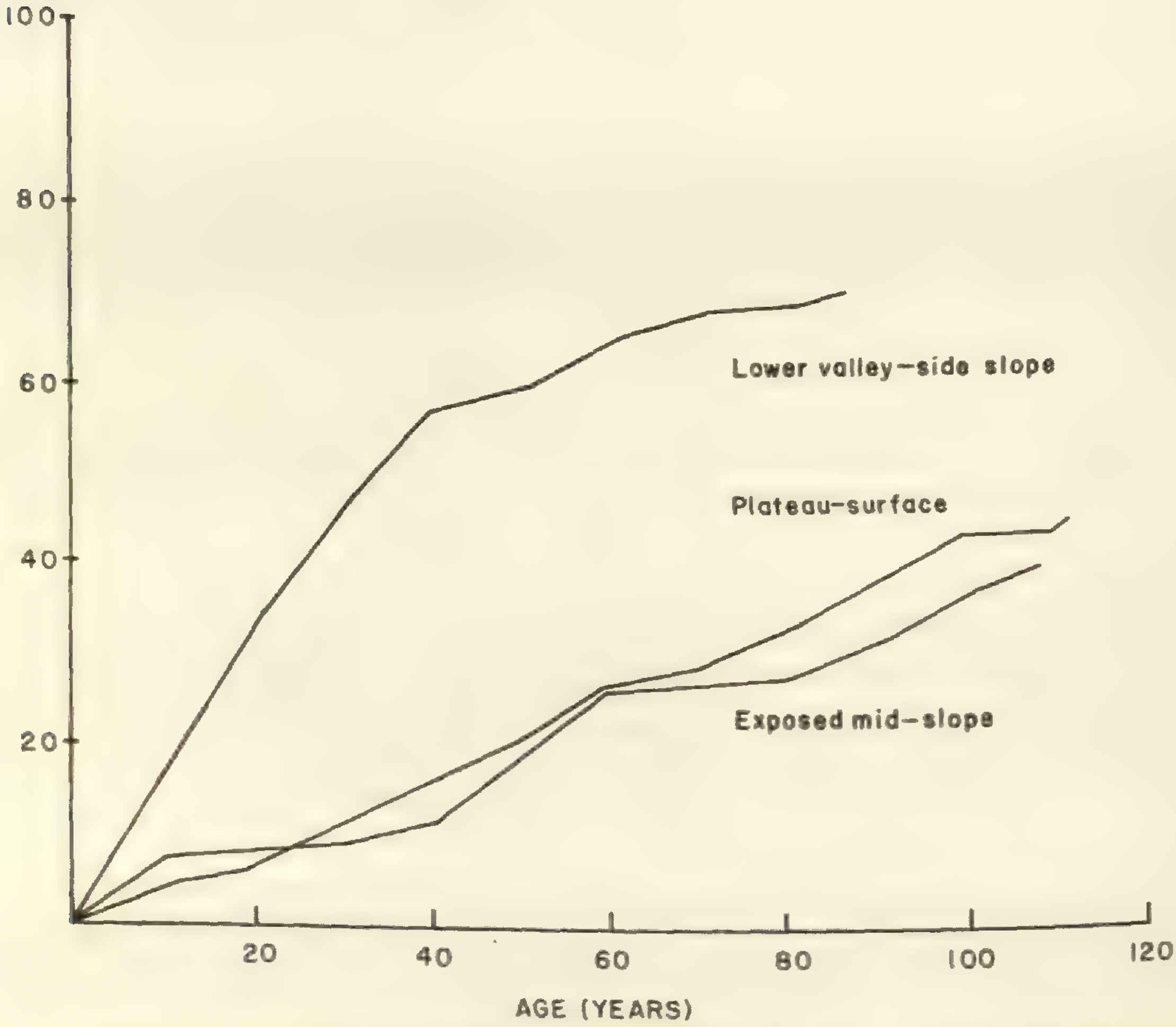

FIGURE 2. Height growth in codominant sugar maples on different sites.

in the foregoing tables, sugar maple, manifesting wide ecological amplitude, is distributed over a considerable segment of the available range of sites.

The species is very common on bottomlands and foot-slopes. On somewhat drier, low-level surfaces such as fans and terraces, the abundance of sugar maple ranges from low to high. Density commonly is high in undisturbed stands occupying the treads of strath terraces and benches. Conversely, species representation is variable but commonly low on the disturbed alluvial fans and terraces of the Northeast Margaree River.

On mid-slopes and crest-slopes in interfluve areas, sugar maple varies widely in density, ranging from a few stems to a high percentage representation per acre. On moist sites at medium and higher elevations (stream-hollows and valley-heads), the density of sugar maple commonly is high and often appreciably greater than on nearby valley-side slopes. On spurs the density of sugar maple is extremely variable, with medium high concentrations of the species often occurring on features of wide lateral extent, and very low densities being encountered on steep, narrow forms.

The density of sugar maple declines rapidly on approaching the altitudinal limits of the range of the species. The "farthest-on" position may be encountered either on the gentle slopes of the plateau surface or on the uppermost segments of steep, valley-side slopes. The apparent limit of sugar maple in northern Cape Breton Island comprises a zone of diffusely scattered trees, with individuals of the species continuing to form part of the forest canopy.

Fowells (1965) has examined the habitat preferences of sugar maple, noting that the species prospers on moist, well-drained sites, and that yield and quality increase with improvement in soil-moisture conditions. Site-density relations in northern Cape Breton Island support the suggestion of a coincidence between the abundance of sugar maple and soil-moisture regimes. In northern Cape Breton, sugar maple is distributed over a broad range of sites and reflects a tendency toward high densities on sites where runoff and seepage water are concentrated and less quickly dispersed. High densities also occur on fresh sites such as stream-hollows, where contours assume a concave-outward configuration, indicating a zone of possible concentration of moisture in the ground. Moderately high densities are to be found on strath terraces and the peripheral reaches of flattish upland surfaces where runoff and seepage water are less quickly dispersed. Low densities of sugar maple are found on sites marked by rapid drainage, such as coarse-textured fans, narrow spurs, and steep mid-slopes and crest-slopes.

A particularly striking aspect of the geography of sugar maple in northern Cape Breton Island is the deterioration in height and form which characterizes the species in passing from protected, moist bottomlands to exposed crest-slopes and the plateau surface. Canopy sugar maples, in a vertical interval of 1000 feet (305 m.) or less, may reflect a reduction in relative height of 50 per cent or more over the foregoing gradient. Accordingly, in the forests of peripheral reaches of the tableland, sugar maple, while continuing as an overstory species, characteristically demon-

strates much reduced height and very poor form on the individual tree level.

A comparison of the behavior of sugar maple on the limits of its range in northern Cape Breton Island with that of the species in like circumstances elsewhere reveals both similarities and differences. Braun (1950) and Dansereau (1943) have commented on the confinement of sugar maple to summits, ridge-tops, and well-drained slopes in northern sections of the hemlock, white pine, northern hardwoods forest of Ontario and southwestern Quebec. Cater (1961) has observed that, on the limits of its range in northwestern New Brunswick, sugar maple is abundant on, and apparently restricted to, hilltops and upper slopes, but is absent from lower slopes and bottomlands. Dansereau (1944) has pointed out that, in the Gaspé Peninsula of Quebec, sugar maple is restricted to gentle slopes at elevations of approximately 200 to 600 feet (61–183 m.) in the interior valleys and on outlying hills of the Shikshok escarpment. Alternatively, Bormann *et al.* (1970) and Siccama (1974), working in the White Mountains of central New Hampshire and the Green Mountains of Vermont, respectively, report distribution and behavior patterns in sugar maple on the limits of its range in those areas which appear to resemble the patterns reflected by the species in northern Cape Breton Island.

Notable features of the geography of sugar maple in close proximity to the limit of its range in northern Cape Breton Island include broad ecological amplitude, relatively high density of stocking and, in protected bottomland sites, impressive stature and vigor on the individual tree level. Salient aspects of the distribution pattern of the species include restriction of the range to a vertical interval of the order of 1000 feet (305 m.) and abrupt altitudinal truncation of the range. Also noteworthy is the status of individual sugar maples on the periphery of the range. The limiting trees are almost invariably codominant members of the overstory, approaching or equaling in height and diameter the dimensions of trees of other species represented in the canopy. Despite the reduction in size and deterioration in form of range-limit trees in comparison with individuals of similar diameters in nearby bottomland sites, there is no suggestion of a decline in stature to a depauperate habit over the elevation gradient, or of a marked decrease in vigor upon approaching the limit of the range of the species.

The factors which control or which have contributed to the present pattern of distribution of sugar maple in northern Cape Breton Island are not clearly defined. As noted in a previous paper (Greenidge, 1972), the present altitudinal limit does not appear to be linked to topographic or edaphic changes or discontinuities. Putative climatic effects are suggested by unthriftiness in sugar maple regeneration at elevations slightly exceeding the altitudinal limits of nearby canopy trees, and by differences in the altitudinal limit on seaward-facing versus inland sites (Greenidge, 1972). Likewise, competition may be a factor restricting the spread of sugar maple at higher elevations in the region. Similarly, historical fac-

tors, particularly Pleistocene and post-Pleistocene events, may be of great significance to the contemporary patterns of distribution of sugar maple in the area.

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A REVISION OF THE PAPUASIAN SPECIES OF ACMENA (MYRTACEAE)

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In the most recent taxonomic work dealing with the Papuasian species of *Acmena* DC. (Merrill & Perry, 1938 & 1942), six species were recognized for the area: four endemic, *A. dielsii* Merr. & Perry, *A. dispansa* (Ridley) Merr. & Perry, *A. laevifolia* (Ridley) Merr. & Perry, and *A. polyantha* (Lauterb. & K. Schum.) Merr. & Perry; one Indo-Malesian, *A. acuminatissima* (Bl.) Merr. & Perry; and one common to western Papua New Guinea and eastern Australia, *A. hemilampra* (F. Muell. ex F. M. Bailey) Merr. & Perry. At the time these studies were made, only a very few Papuasian collections of *Acmena* were available (six were cited in the former paper and eight were cited in the latter); thus it is not surprising that now, with nearly eight times the number of collections at hand, we can see the need for some changes and additions.

We are of the opinion that three of the species Merrill and Perry recognized, *A. dielsii*, *A. laevifolia*, and *A. polyantha*, are more correctly placed in synonymy, and we recognize, among collections that have been made since their studies, three new species. In addition, we have found that the Papuasian *Syzygium triphlebium* Diels, which was accepted in *Syzygium* by Hartley and Perry (1973), is more correctly placed in *Acmena*, and that *Syzygium acmenoides* Merr. & Perry, which was informally referred to *Acmena* by Hartley and Perry (1973: 220), is correctly placed in *Syzygium*. The purpose of this paper is to revise the Papuasian species of *Acmena* in view of this new information.

As Merrill and Perry pointed out (1938), *Acmena* ranges from mainland Asia throughout Malesia to the Solomon Islands and south to northern and eastern Australia. We have restricted this study to the Papuasian species because we believe it is advisable to study *Acmena* in conjunction with *Syzygium*, and our work on the latter genus, continuing that of Hartley and Perry (1973), is limited to that region. The Australian species of *Acmena* and *Syzygium* are being studied by B. P. M. Hyland, C.S.I.R.O. Division of Forest Research.

Specimens cited in this paper are deposited at the British Museum (Natural History), London (BM), the Queensland Herbarium, Brisbane (BRI), the C.S.I.R.O. Herbarium Australiense, Canberra (CANB), and the Rijksherbarium, Leiden (L). We wish to thank the directors and curators of these herbaria for making specimens in their care available to us. Thanks are also extended to the curator and staff of the Canberra Botanic Gardens for the opportunity to study living material of *Acmena smithii* (Poiret) Merr. & Perry.

Acmena DC. Prodr. 3: 262. 1828. (For details of generic typification and synonymy see Merrill & Perry (1938) and Johnson, Contrib. New S. Wales Natl. Herb. 3: 100. 1962.)

Lomastelma Raf. Sylv. Tellur. 107. 1838 (reference not seen).
Xenodendron Lauterb. & K. Schum. in K. Schum. & Lauterb. Fl. Deutsche Schutzgebiete Südsee 461. *t. 16.* 1900.

Trees or shrubs; buds with scales completely enclosing the leaf and floral primordia. Leaves opposite or subopposite, simple, oil-dotted, entire, with open venation (as defined by Hartley & Perry, 1973: 175), main veins confluent near the leaf margin to form one or two intramarginal veins. Inflorescences terminal and/or from the axils of the upper leaves, paniculate. Flowers bisexual; calyx tube turbinate to funnel-shaped; calyx lobes 4 or 5, minute or obsolete; petals 4 or 5, distinct, imbricate, caducous; stamens numerous, apparently in 2 or 3 series at the top of the hypanthium; filaments flexuous, of various lengths, those of the inner series of stamens shortest, those of the outer series longest; anthers minute; anther sacs globose or subglobose, divaricate, apically dehiscent by a pore or slit; ovary inferior, 2-locular; placentation upper axile; ovules (3–) 5–19 per locule, campylotropous, pendulous, elongate; style 1, straight, stigma scarcely differentiated. Fruit drupaceous, globose, with fleshy mesocarp and subwoody endocarp. Seed 1, globose; testa and endosperm absent; cotyledons 2, chlorophyllous, oil-dotted, thickened, enclosing an intrusive, ramifying mass of placental tissue, outer surfaces plane, inner surfaces ruminate and interlocked with the placental tissue; hypocotyl minute, external or slightly internal; epicotyl with two scale leaves.

The structure of the seed of *Acmena* is very unusual and has been variously interpreted (see Merrill & Perry, 1938: 6, 7, who also discuss some earlier references; Henderson, 1949: 10. *fig. 5*; and Kausel, 1957: 607, 608). We have studied the development of the seed from the ovule through to maturity and germination, using, to a large extent, living material of the Australian endemic *A. smithii*. We have concluded that it lacks a testa and endosperm, and that the cotyledons, at least in *A. smithii*, are distinct. The cotyledons enclose a branching mass of tissue which appears to be placental in origin and function. Details of this development are given below and are illustrated in FIGURE 1.

FIGURE 1. Seed development in **Acmena smithii** (Poiret) Merr. & Perry. a, longitudinal section of flower at anthesis. b, seed at early stage of development (removed from ovary). Shown are the hilum-like area of placental tissue, the aborted ovules, and the "integument" (partially stippled), which surrounds the embryo at this early state. c, seed at later stage of development (removed from young fruit). One cotyledon has been removed. Shown are the remaining cotyledon (non-shaded) with attached hypocotyl and the two scale leaves of the epicotyl, the branching mass of intercotyledonary placental tissue, and, continous with it, the hilum-like area of placental tissue. d, longitudinal section of the mature fruit (diagrammatic). Shown are the outer, fleshy portion of the fruit (non-shaded), the subwoody endocarp (hatched), and the seed, the latter consisting of a naked embryo (non-shaded) and a branching mass of placental tissue (dark-shaded). A portion of the line of demarcation between the two cotyledons is shown at the lower end of the embryo.

a
1mm.
TGH

b
1mm.

c
1mm.

d
5mm.

In the flower at anthesis (FIGURE 1a), the ovules are attached to a four-lobed, upper-axile placenta, two lobes of which protrude into each of two locules. The vascular supply to the placenta is in the form of a single strand which extends from the base of the flower up through the center of the ovary. According to Schmid (1972: 451. *figs. 3–16*), in a study which includes a detailed account of the floral anatomy of *Acmena smithii*, this strand consists of numerous vascular bundles. The ovules, which are usually about 14 per locule in *A. smithii*, are elongate, pendulous, and sessile. Each locule is bounded by a tissue that is compact in comparison to the surrounding ovary tissue, which is spongy.

Following fertilization, a single ovule of the flower develops into a seed. As this development progresses, the locule containing the developing seed enlarges and becomes central-apical in its position in the ovary. The other locule, containing only aborted ovules, is flattened against the upper side of the expanding locule. At the point of attachment of the developing seed, the placenta enlarges and, in part, appears to grow through the funicular region and into the embryo sac. At the stage illustrated in FIGURE 1b (which shows a very young seed removed from the locule), this placental tissue is visible externally as a broad, hilum-like structure. Internally, it has grown part way between the cotyledons of the developing embryo and has begun to branch. Enclosing the embryo, but not the "hilum," is a thin, delicate tissue which is probably a single integument. External to this "integument," and attached to the "hilum," are the aborted ovules of the locule. At this stage, the embryo consists of two separate, suborbicular cotyledons and an external hypocotyl. There is no evidence that endosperm is formed.

As development continues, the cotyledons and the inter-cotyledonary mass of placental tissue enlarge, and the latter becomes increasingly complex in its branching. Early in this enlargement the "integument" is sloughed off. At the stage of development shown in FIGURE 1c, the "integument" has disappeared, the cotyledons are still quite distinct and are easily separable, both from one another and from the intercotyledonary placental material, and the hypocotyl and two scale leaves of the epicotyl are visible at the lower end of the developing embryo.

As the seed approaches maturity, the embryo, in conforming with the irregularities of the increasingly branching intercotyledonary material, grows more and more unevenly. As a result, the external line of demarcation between the two cotyledons, which was fairly straight in the early stages of seed development, becomes increasingly distorted and difficult to follow. Also, the cotyledons become interlocked, or dovetailed, with the intercotyledonary material. This dovetailing usually makes it impossible to separate the cotyledons from the intercotyledonary material without tearing them. We have not seen evidence, however, that the cotyledons themselves are actually grown together (conferruminate), as most previous authors have thought. A further result of the uneven growth of the embryo is that the position of the hypocotyl may be altered; thus in some seeds it is external and in others it is slightly internal.

We may be incorrect in referring to the intercotyledonary material as placental. Nevertheless, it seems to be continuous, throughout its development, with the tissue to which the ovules are attached. Also, it contains branching vascular tissue that is continuous with the axile vascular strand of the flower, and, in its close and intricate contact with the inner faces of the cotyledons, it provides an extensive surface for the possible diffusion of food into the developing embryo.

The fleshy mesocarp of the fruit is derived from the calyx tube, and the subwoody endocarp develops mainly from the ovary wall (FIGURE 1d). The fruits of *Acmena* are eaten by birds (including, in north Queensland, the cassowary, *Casuarius casuarius*; the top-knot pigeon, *Lopholaimus antarcticus*; the wompoo pigeon, *Ptilinopus magnificus*; and the purple-crowned pigeon, *Ptilinopus superbus* — Frank Crome, C.S.I.R.O. Division of Wildlife Research, pers. comm.). It is probable that the endocarp prevents digestion of the seed.

During seed germination, which is hypogeal, the cotyledons remain together, closely interlocked with the intercotyledonary placental material. Under natural conditions, germination does not occur until the endocarp has sufficiently softened or rotted away to allow emergence of the root and shoot of the seedling. The scale leaves do not enlarge appreciably upon germination and appear at the first node of the seedling. Two additional nodes of similar scale leaves appear before the seedling produces a pair of functional foliage leaves at the fourth node.

The cotyledons apparently provide food for the developing seedling; the intercotyledonary material does not seem to have a nutritive function at this stage. By the time the seed has reached maturity, it is composed, apparently entirely, of non-living tissue. In this final state it is remarkably similar in texture and color to the carpellary dissepiments (which are also placental in origin) to which the seeds are attached in the fruits of *Flindersia* (Rutaceae), being hard, brittle, and dark reddish brown in color.

The closest generic affinities of *Acmena* appear to be found in *Acmenosperma* Kausel, a recently described monotypic genus based on the Indo-Malesian *Eugenia claviflora* Roxb. (*Syzygium claviflorum* (Roxb.) Cowan & Cowan), and *Piliocalyx* Brongn., a genus of nine species, eight endemic to New Caledonia and one endemic to Fiji. The seeds of both of these genera are similar to those of *Acmena*, having branching intercotyledonary placental tissue. *Acmena*, *Acmenosperma*, and *Piliocalyx* may be distinguished as follows:

1. Calyx tube calyptrate at the summit. ..... *Piliocalyx.*
1. Calyx tube lobed or undulate at the summit.
   2. Anther sacs globose or subglobose, divaricate, apically dehiscent by a pore or slit. ..... *Acmena.*
   2. Anther sacs elongate, parallel, laterally dehiscent by a longitudinal slit. ..... *Acmenosperma.*

Kausel (1957) has proposed (but apparently not validly published) a new subfamily, the Acmenoideae, for these three genera. We agree that

they seem to form a natural group, but doubt that they occupy a sufficiently remote evolutionary position from *Syzygium* to warrant placement in a separate subfamily. *Acmenosperma claviflora* (Roxb.) Kausel seems to stand in an intermediate position between *Acmena* and *Syzygium sensu stricto*, having the basic seed structure of the former and the anther characteristics of the latter.

Measurements given in the taxonomic section which follows are all based on dried material. It should be noted that mature fruits shrink to about one half their fresh size with drying. The flower and fruit colors given are based on collectors' notes.

The descriptions of the two species which are also known outside Papuasia, *Acmena acuminatissima* and *A. hemilampra*, are based only on Papuasian specimens.

We have not been able to arrange the species in a phylogenetic sequence, nor are we at all sure of their interrelationships. For these reasons we have arranged them alphabetically in the taxonomic section. We suspect, as did Merrill and Perry (1938), that fruit and seed characteristics might provide a basis for a natural classification, but the material at hand is unsuitable for a detailed and comprehensive study of these organs. Besides shrinking, as mentioned above, the fruits of the Papuasian species become extremely hardened with drying and are very difficult to work with, even after prolonged soaking and boiling.

KEY TO THE SPECIES
(based on flowering material)

1. Calyx tube 6–10 mm. long.
   2. Leaf blades lanceolate, 20–45 cm. long, 4.5–11 cm. wide, main veins 12–16 on each side of the midrib. ..... 6. *A. sorongensis.*
   2. Leaf blades elliptic or occasionally sublanceolate, (12–)15–33 cm. long, (4.5–)7–16 cm. wide, main veins 7–10(–16) on each side of the midrib. ..... 5. *A. montana.*
1. Calyx tube 2.5–5 mm. long.
   3. Leaf blades 5–10 cm. long.
      4. Calyx tube 4–5 mm. long; leaf blades narrowly elliptic, at least 6 times as long as broad, apex acuminate. Rheophyte. ..... 3. *A. fluvicola.*
      4. Calyx tube 3–4.5 mm. long; leaf blades not more than 4 times as long as broad.
         5. Leaf blades elliptic to subobovate, apex obtuse to shortly and bluntly acuminate. ..... 4. *A. hemilampra.*
         5. Leaf blades lanceolate to elliptic, apex acuminate to cuspidate. ..... 1. *A. acuminatissima.*
   3. Leaf blades 10–24 cm. long.
      6. Veins conspicuously paler than the brownish leaf blade surface; calyx tube 2.5–3 mm. long. ..... 7. *A. triphlebia.*
      6. Veins not conspicuous as above; calyx tube 3–5 mm. long.
         7. Leaf blades drying glossy dark brown above, main veins about 12 on each side of the midrib; calyx tube 3 mm. long. ..... 2. *A. dispansa.*

7. Leaf blades usually drying dull grayish above, main veins 7–15 on each side of the midrib; calyx tube 3–5 mm. long. . . . . 1. *A. acuminatissima.*

Key to the Species
(based on fruiting material [1])

1. Leaf blades 5–10 cm. long.
   2. Leaf blades more than 6 times as long as broad. . . . . 3. *A. fluvicola.*
   2. Leaf blades less than 4 times as long as broad.
      3. Leaf blades elliptic to subobovate, apex obtuse to shortly and bluntly acuminate. . . . . 4. *A. hemilampra.*
      3. Leaf blades lanceolate to elliptic, apex acuminate to cuspidate. . . . . 1. *A. acuminatissima.*
1. Leaf blades more than 10 cm. long.
   4. Mature fruits white or cream.
      5. Veins conspicuously paler than the brownish leaf blade surface, main veins about 10 on each side of the midrib; mature fruiting pedicels about 1 mm. wide; mature fruits about 1 cm. wide. . . 7. *A. triphlebia.*
      5. Veins not conspicuous as above, leaf blade usually drying dull grayish above, main veins 7–15 on each side of the midrib; mature fruiting pedicels 1–10 mm. wide; mature fruits 1.5–4 cm. wide. . . . . 1. *A. acuminatissima.*
   4. Mature fruits red or pink.
      6. Leaf blades lanceolate, 20–45 cm. long, 4.5–11 cm. wide, main veins 12–16 on each side of the midrib. . . . . 6. *A. sorongensis.*
      6. Leaf blades elliptic or occasionally sublanceolate, (12–)15–33 cm. long, (4.5–)7–16 cm. wide, main veins 7–10(–16) on each side of the midrib. . . . . 5. *A. montana.*

1. **Acmena acuminatissima** (Bl.) Merr. & Perry, Jour. Arnold Arb. 19: 12. 1938.

Myrtus acuminatissima Bl. Bijdr. 1088. 1826. Type: *Blume*, Java (not seen). (For other extra-Papuasian synonyms of *Acmena acuminatissima*, see Merrill & Perry, 1938.)

Xenodendron polyanthum Lauterb. & K. Schum. in K. Schum. & Lauterb. Fl. Deutsche Schutzgebiete Südsee 461. *t. 16.* 1900. Type: *Bamler 5*, Northeast New Guinea, Sattelburg (not seen).

Eugenia laevifolia Ridley, Trans. Linn. Soc. Bot. II. 9: 48. 1916. Type: *Kloss* (*Wollaston Expedition*), 1912–1913, West New Guinea, southern slopes of the Nassau Range.

Acmena polyantha (Lauterb. & K. Schum.) Merr. & Perry, Jour. Arnold Arb. 19: 11. 1938.

Acmena dielsii Merr. & Perry, *loc. cit.*: 18. Type: *Brass 675*, Papua, Gawarere.

Acmena laevifolia (Ridley) Merr. & Perry, *loc. cit.*: 18, 19.

Shrub or small to large tree to about 30 m.; branchlets glabrous to puberulent to finely pubescent, terete or compressed or rarely tetragonous,

[1] We have not seen fruits for species 2, 3, and 4, *A. dispansa, A. fluvicola,* and *A. hemilampra.* With the exception of *A. dispansa,* however, we have included them in this key since they are distinguishable by leaf characters.

1–5 mm. wide. Leaves entirely glabrous or puberulent to finely pubescent on the petiole and lower midrib; petiole 5–10 mm. long, 1–3 mm. wide; leaf blade chartaceous to subcoriaceous, usually drying grayish above, brownish below, usually dull on both surfaces, broadly to narrowly elliptic to lanceolate, (4–)9–21(–24) cm. long, (1.5–)2–7.5 cm. wide, base rounded to cuneate, apex acuminate to cuspidate. Inflorescences terminal or terminal and from the axils of the upper leaves, to about 15 cm. long, axis and branches glabrous to puberulent to finely pubescent. Flowers white; calyx tube 3–5 mm. long, at the base narrowed into a stipe 1.5–2 mm. long, at the apex 2–4 mm. wide; calyx lobes 0.25–0.5 mm. high; petals orbicular, 1–2 mm. wide; stamens 0.5–2 mm. long. Mature fruiting pedicels 1–10 mm. wide; mature fruits white, 1.5–4 cm. wide.

ILLUSTRATIONS. Engler, A., & K. Prantl, Nat. Pflanzenfam. Ergänzungsh. 2: 239. *fig. 33*. 1907 (as *Xenodendron polyanthum* Lauterb. & K. Schum.). Henderson, M. R., Gard. Bull. Singapore 12: 9. *fig. 4*; 263. *fig. 51a*; 264. *fig. 52*. 1949 (all as *Eugenia cumingiana* Vidal). Koorders, S. H., & Th. Valeton, Atlas der Baumarten von Java 3: *t. 506*. 1915 (as *Eugenia acuminatissima* Kurz). Lauterbach, C., & K. Schumann in K. Schumann & C. Lauterbach, *loc. cit.*

DISTRIBUTION. Irian Jaya, Papua New Guinea (including New Britain and Bougainville), and the Solomon Islands (also in western Malesia and mainland Asia, *fide* Merrill & Perry, 1938); primary and regrowth rain forests; usually in lowlands and foothills, but occasionally at higher elevations up to 2400 meters.

Irian Jaya. Vogelkop Peninsula, Oransbari, *Kokkelink BW 2293* (CANB); southern slopes of Nassau Range, Utakwa River, Camp 1, *Kloss (Wollaston Expedition)*, 1912–1913 (BM, holotype of *Eugenia laevifolia* Ridley); Bele River, 18 km. NE of Lake Habbema, *Brass & Versteegh 11142* (BRI); vicinity of Hollandia, mouth of Tami River, *Kalkman BW 3443* (CANB); vicinity of Hollandia, Lake Sentani, *van der Sijde BW 4001* (CANB). **Papua New Guinea.** SEPIK DISTRICT: Vanimo Subdistrict, about 1 km. from Ossima airstrip, *Katik NGF 46699* (BRI, CANB); Kokomo Creek, tributary of Frieda Creek, *Henty & Foreman NGF 42662* (BRI, CANB); near Ambunti, *Hoogland & Craven 10177* (CANB). EASTERN HIGHLANDS DISTRICT: Arona side of Kassam Pass, *Womersley NGF 46426* (CANB). MOROBE DISTRICT: Boana, *Clemens 8233A* (CANB); Sankwep River, *Womersley NGF 43722* (CANB); Busu River, *Henty NGF 12416* (BRI, CANB); Burep [Bupu] River NE of Lae, *Hartley 10117* (CANB), *10134* (CANB), *Millar NGF 12283* (BRI); Bunga River about 24 km. NE of Lae, *Hartley 12285* (BRI, CANB); near the Butibum River about 11.2 km. N of Lae, *Hartley 11444* (CANB); 24 km. W of Lae, *Streimann & Kairo NGF 47718* (CANB); Oomsis Creek 28.8 km. W of Lae, *Hartley 10040* (CANB), *Henty NGF 14369* (BRI, CANB); 4.8 km. S of the Garagos River bridge on Lae-Bulolo Road, *Hartley 11025* (CANB); Patep River, about 6.4 km. S of Gurukor, *Hartley 11000* (CANB); Edie Creek Road near Blue Point, *Havel & Kongara NGF 17322* (BRI, CANB); Kui, *Henty NGF 28095* (BRI); Posei village, 16 km. SW of Morobe, *Streimann NGF 24081* (CANB). NEW BRITAIN: Mt. Talawe, *Ridsdale NGF 30528* (BRI), *Frodin NGF 26838* (BRI, CANB); NE of Aisega village, *Frodin NGF 26696* (BRI, CANB); Cape

Hoskins, Malalia, *Floyd NGF 6553* (BRI, CANB). BOUGAINVILLE: lower south slopes of Lake Loloru crater, about 22 km. N of Buin, *Craven & Schodde 269* (CANB); vicinity of Barilo village, about 9.5 km. N of Buin Station, *Schodde & Craven 3964* (CANB); Siwai, *Waterhouse 128–B* (BRI, CANB), *475–B* (BRI). SOUTHERN HIGHLANDS DISTRICT: Anga Valley, near Ebenda, *Schodde 1539* (CANB). WESTERN DISTRICT: lower Fly River, east bank opposite Sturt Island, *Brass 7977* (BRI). CENTRAL DISTRICT: Tapini, *Lelean NGF 46390* (CANB); Isuarava, *Carr 15880* (CANB); Gawarere, *Brass 675* (BRI, isotype of *Acmena dielsii* Merr. & Perry); Kuriva Forestry Area, near Veimauri River, *Streimann & Kairo LAE 51516* (CANB); Brown River near Karema, *Schodde 2607* (CANB); Boridi, *Carr 14805* (CANB); Cape Rodney, near P.I.T. sawmill, T.P. 107, *Henty NGF 38613* (BRI, CANB). NORTHERN DISTRICT: Pongani Valley, between Dareki and Ondoro, *Pullen 5677* (CANB). MILNE BAY DISTRICT: eastern Mt. Simpson Range, Mt. Moiba, *Schodde 5356* (CANB). **Solomon Islands.** Guadalcanal, Tutuve Mountain, Unloto, *Kajewski 2553* (BRI).

As we interpret it, *Acmena acuminatissima* is polymorphic in Papuasia. Among the collections at hand, we can recognize three major entities, but for various reasons (discussed below) we prefer not to recognize any of them formally. It should be noted that Merrill and Perry (1938) saw very little of the variability that has led us to this much more conservative circumscription of this species. They cited only one Papuasian collection, *Kajewski 2553*, for *A. acuminatissima*, and, of the names we have placed in its synonymy, they only had fragments (of two collections) of *A. polyantha*, a single collection of *A. dielsii*, and a single flower of *A. laevifolia*.

Entity 1. Branches of the inflorescences (and often the branchlets, petioles, and lower midrib of the leaves) finely pubescent to puberulent; mature fruiting pedicels about 2.5 mm. wide; mature fruits about 2.5 cm. wide; leaf blades narrowly to broadly lanceolate or occasionally elliptic, 7.5–11 cm. long, acuminate to cuspidate at the apex; flowers with calyx tube 3–4.5 mm. long.

Seven of the collections cited above (and also the type collection of *Xenodendron polyanthum*) can be readily placed in this entity. These are *Clemens 8233A*, *Hartley 10117*, *10134*, *11000*, and *12285*, and *Streimann & Kairo NGF 47718*, all from the Morobe District; and *Carr 15880*, from the Central District. Seeming to grade toward a glabrous condition are *Hoogland & Craven 10177*, from the Sepik District, and *Brass 7977*, from the Fly River, both of which are only minutely puberulent; and *Kokkelink BW 2293*, from the Vogelkop, which is only minutely papillate (visible at about 20×). Examination of the variations in these vestiture types in single specimens reveals that there is complete intergradation from finely pubescent to puberulent to minutely papillate. The step from minutely papillate to the glabrous and smooth condition of the remaining Papuasian collections that we have placed in *Acmena acuminatissima* is but a short one, and it is probably safe to say that there is complete intergradation between the pubescent and glabrous plants. Examination of our western Malesian material of *A. acuminatissima* has revealed that two of the collections, *Kostermans & Kuswata 27*, from Java, and *Kos-*

termans 6785, from Borneo, are minutely papillate, while the other collections, which are from the Philippines, Borneo, and the Celebes, are glabrous and smooth. It appears, then, that the tendency toward pubescence may be of sporadic geographic occurrence in this species. We have attempted to find other characters of the pubescent plants which would aid in distinguishing them from those that are glabrous, but there seem to be none.

Entity 2. Plants entirely glabrous; mature fruiting pedicels about 1 mm. wide; mature fruits 1–2 cm. wide; leaf blades lanceolate to broadly elliptic, 5–18 cm. long, acuminate to cuspidate at the apex.

We have four glabrous collections with mature fruits in this size range: *van der Sijde BW 4001*, from Irian Jaya, and *Floyd NGF 6553*, *Frodin NGF 26696*, and *Ridsdale NGF 30528*, all from New Britain. On the basis of descriptions and specimens we have seen, the western Malesian material of *Acmena acuminatissima* closely matches this Papuasian material in fruit size, although there seems to be a difference in the color of the mature fruit. Collectors in Papuasia have invariably described it as white, whereas from Java (Bakhuizen f., Fl. Java 1: 337. 1963) and Malaya (Ridley, Fl. Malay Penin. 1: 747. 1922, and Henderson, 1949: 262) it has been described as being various shades of blackish red. It is probably also worth mentioning that *A. acuminatissima* is described as having stilt roots in Java (Bakhuizen f., *loc. cit.*), and as sometimes having them in Malaya (Henderson, 1949: 261). The presence of such roots was noted with the Frodin collection placed in this entity, and also with the type collection of *A. dielsii*, *Brass 675*, from the Central District, Papua New Guinea, a glabrous flowering collection not assigned to an entity.

Entity 3. Plants entirely glabrous; mature fruiting pedicels 5–10 mm. wide; mature fruits 3–4.5 cm. wide; leaf blades lanceolate to rather broadly elliptic, 12–22 cm. long, acuminate at the apex.

Glabrous Papuasian collections with fruits in this size range are as follows: *Hartley 10040*, *Henty NGF 12416*, *Millar NGF 12283*, *Streimann NGF 24081*, and *Womersley NGF 43722*, all from the Morobe District; and *Lelean NGF 46390*, *Schodde 1539* and *5356*, and *Streimann & Kairo LAE 51516*, all from the southern part of Papua New Guinea. In the large fruits and heavy, woody fruit stalks, these plants are strikingly different from those placed in Entity 2. We have not been able to correlate the fruit size differences with other characters, however.

Thus, we can readily sort pubescent plants into Entity 1, and glabrous fruiting collections into either Entity 2 or Entity 3. We have not been able to sort glabrous flowering collections, however, and these collections include the type collections of *Acmena dielsii* and *A. laevifolia*. The flowers of the glabrous material appear more or less identical except for size differences. The calyx tube ranges in length, without significant discontinuity, from 3 to 5 mm. We have one small-fruited collection with

both flowers and fruits, *van der Sijde BW 4001*, listed above under Entity 2. In this collection, the fruits are about 1 cm. wide and the flowers, which are in bud but appear to be nearly at anthesis, have a calyx tube about 4 mm. long. In the large-fruited entity there are no collections with both flowers and fruits. We are quite certain, however, that the flowering stage is represented by *Henty NGF 14369*, from Oomsis Creek, near Lae, because from that same locality we have a large-fruited collection, *Hartley 10040*, which is a good match vegetatively. The flowers of the Henty collection have a calyx tube 3.5–4 mm. long and they are not significantly different from those of the small-fruited van der Sijde collection. The leaves of the glabrous flowering collections range across the spectrum of shapes and sizes given above for Entities 2 and 3.

On the basis of the data given by collectors and our field experience in Papuasia, there is no reliable evidence of ecological specialization in the three entities of *Acmena acuminatissima*. They all appear to grow in both primary and regrowth rain forests over a fairly wide altitudinal range.

We have two collections, one from Irian Jaya (*Brass & Versteegh 11131*, Bele River, 18 km. NE of Lake Habbema, tree 20 m. tall in montane rain forest) and one from Papua New Guinea (*Craven & Schodde 1245*, Morobe District, Aseki Patrol Area, tree 28 m. tall in montane rain forest), that seem to be closely related to *A. acuminatissima* but differ in having narrower leaves (about 5 times as long as broad) and pustulate, as opposed to smooth or minutely papillate, inflorescence branches. We think they represent a distinct species, but their localities are so far apart (nearly 800 kilometers) that it seems best to defer formal recognition until more material is available. There are two other collections that may belong here: *Henty & Foreman NGF 42662*, from the Sepik District, which is in very early bud; and *Kalkman BW 6372*, from the Vogelkop Peninsula, which is sterile. The four collections are listed in the Index to Exsiccatae as *Acmena* aff. *acuminatissima*.

There are two further collections that are of uncertain identity which we have listed in the Index to Exsiccatae as *Acmena* aff. *acuminatissima*: *Streimann & Kairo, NGF 39397*, Morobe District, Wau Subdistrict, Palenkwa, Golden Pines, tree 24 m. tall in *Araucaria* forest; and *Womersley NGF 24926*, Eastern Highlands District, Okasa, canopy or emergent tree 33 m. tall in lower montane rain forest. Both of these collections have only immature fruits, but in the size of the fruiting pedicel they appear to belong to the large-fruited Entity 3 of *A. acuminatissima*. The leaves, however, tend to be obovate, which sets them apart from that species.

2. **Acmena dispansa** (Ridley) Merr. & Perry, Jour. Arnold Arb. 19: 18. 1938.

Eugenia dispansa Ridley, Trans. Linn. Soc. Bot. II. 9: 47. 1916. TYPE: *Kloss* (*Wollaston Expedition*), 1912–1913, West New Guinea, southern slopes of Nassau Range.

Tree(?); branchlets glabrous, terete, 1.5–2 mm. wide. Leaves glabrous; petiole 6–8 mm. long, 1.5–2 mm. wide; leaf blade subcoriaceous, drying

glossy dark brown above, duller and paler below, narrowly elliptic to lanceolate, 10–20 cm. long, 2.5–4.5 cm. wide, base obtuse to acute, apex acuminate, main veins about 12 on each side of the midrib, prominent. Inflorescences terminal, to about 20 cm. long, glabrous. Flowers white (*fide* Ridley); calyx tube 3 mm. long, at the base narrowed into a stipe about 1 mm. long, at the apex 2 mm. wide; calyx lobes about 0.3 mm. high; petals orbicular, about 1 mm. wide; stamens 0.5–1 mm. long. Fruits not seen.

DISTRIBUTION. Known only from the type collection.

Irian Jaya. Southern slopes of Nassau Range, near Tsingarong River, Camp VIa and Camp VIc, alt. 900–1700 m., *Kloss (Wollaston Expedition)*, 1912–1913 (BM, holotype).

A collection from Ambon Island, in the Moluccas, *Kuswata & Soepadmo 257*, may also be this species.

The closest relative of *Acmena dispansa* may be *A. triphlebia*. Both have similarly brown leaves (when dry) and their flowers are of about the same size and color. They differ mainly in that the latter has paler veins.

3. **Acmena fluvicola** Hartley & Craven, sp. nov. FIGURE 2.

Arbor gracilis usque ca. 5 m. alta; ramulis glabris, teretibus vel compressis, 1–2 mm. latis; foliis glabris; petiolo 5–8 mm. longo, ca. 1 mm. lato; lamina subcoriacea, in sicco supra nitida cinereo-brunnea, subtus obscure brunnea, anguste elliptica, 7–9 cm. longa, 1–1.3 cm. lata, basi cuneata, apice acuminata, venis primariis utrinsecus costa ca. 12, inconspicuis; inflorescentiis terminalibus et ex axillis foliatis superioribus orientibus, glabris, usque ca. 2.5 cm. longis; floribus albis; tubo calycis 4–5 mm. longo, basi stipitato (stipite 2–3 mm. longo), apice 2.5 mm. lato; lobis calycis 0.25–0.5 mm. altis; petalis orbicularibus, ca. 1 mm. latis; staminibus 0.5–1 mm. longis; fructibus non visis. HOLOTYPUS: *Brass 28857* (CANB).

DISTRIBUTION. Known only from the type collection.

Papua New Guinea. MILNE BAY DISTRICT: Dawa Dawa River, along floodbank, alt. 10 m., *Brass 28857* (CANB, holotype).

Acmena fluvicola has willow-like leaves and appears to be restricted to stream banks. As far as we know it is the only rheophyte in the genus. We are at a loss to say what its closest relative might be; although there is a resemblance to the narrow-leaved plant referred to above as *Acmena* aff. *acuminatissima*, it seems to be superficial. The latter is not a rheophyte and has more conspicuous veins and pustular, as opposed to smooth, inflorescence branches.

4. **Acmena hemilampra** (F. Muell. ex F. M. Bailey) Merr. & Perry, Jour. Arnold Arb. **19**: 15. 1938.

Eugenia hemilampra F. Muell. ex F. M. Bailey, Frag. Phytogr. Austral. **9**: 145. 1875 (name merely proposed); Synop. Queensl. Fl. Suppl. **1**: 23. 1886.

FIGURE 2. **Acmena fluvicola** Hartley & Craven. Flowering branchlet, lower surfaces of two leaves shown (drawn from *Brass 28857*).

SYNTYPES (none seen): *Moore*, New South Wales, Clarence River; *Hodgkinson*, New South Wales, Richmond River; *Carron*, New South Wales, Tweed River; *Thozet*, Queensland. Rockhampton; *Nernst*, Queensland, Mackay; *Dallachy*, Queensland, Rockingham Bay; *Curdie & Moore*, Queensland, Cape Sidmouth; *Hill*, Queensland, Russell River and Mt. Bellenden Ker; *Damel*, Queensland, Cape York.

Small to large tree to about 30 m. tall; branchlets glabrous, terete or compressed, 1–2 mm. wide. Leaves glabrous; petiole 5–10 mm. long, 1–2 mm. wide; leaf blade subcoriaceous, drying brownish (often slightly grayish above), somewhat glossy above, dull below, elliptic to subobovate, 5–10 cm. long, 1.5–3.5 cm. wide, base acute to cuneate, apex obtuse to shortly and bluntly acuminate, main veins 8–10(–12) on each side of the midrib, rather obscure. Inflorescences terminal and from the axils of the upper leaves, to about 10 cm. long, glabrous. Flowers white or cream; calyx tube 3–3.5 mm. long, at the base narrowed into a stipe about 2 mm. long, at the apex 1.5–2 mm. wide; calyx lobes obsolete to 0.1 mm. high; petals orbicular, about 1 mm. wide; stamens 0.5–1 mm. long. Fruits not seen.

DISTRIBUTION. Papua New Guinea, Fly River region (also in eastern Australia from Cape York Peninsula south to northeastern New South Wales, *fide* Merrill & Perry, 1938); gallery forests, rain forests, and woodlands; 15–30 meters.

Papua New Guinea. WESTERN DISTRICT: Lake Daviumbu, *Brass 7766* (BRI), *7941* (BRI); near Weam, *Paijmans 389* (CANB), *Ridsdale & Galore NGF 33718* (CANB); Tarl River, branch of Bensbach River, *Paijmans 349* (CANB), *Ridsdale & Galore NGF 33712* (CANB); near Morehead Patrol Post, *Pullen 7147* (CANB); Lower Fly River, Gaima, *Brass 8283* (BRI); Oriomo River, *Womersley & Havel NGF 17710* (BRI, CANB).

Acmena hemilampra does not appear to be closely related to any of the other Papuasian species of the genus.

5. Acmena montana Hartley & Craven, sp. nov.

Arbor parva usque ca. 18 m. alta vel frutex; ramulis glabris, teretibus vel compressis, 2–5 mm. latis; foliis glabris; petiolo 7–10(–20) mm. longo, 2–4 mm. lato; lamina coriacea, in sicco obscure brunnea vel interdum cinerascenti, elliptica vel interdum sublanceolata, (12–)15–33 cm. longa, (4.5–)7–16 cm. lata, basi rotundata vel acuta, apice acuminata, venis primariis utrinsecus costa 7–10(–16), plerumque prominentibus; inflorescentiis terminalibus et ex axillis foliatis superioribus orientibus, usque ca. 20 cm. longis, glabris; tubo calycis rubro vel roseo, 6–10 mm. longo, basi stipitato (stipite 2–3 mm. longo), apice 3.5–4 mm. lato; lobis calycis 0.5–0.75 mm. altis; petalis rubris vel roseis, orbicularibus, 2–3 mm. latis; staminibus albis vel cremeis, 0.75–2 mm. longis; pedicellis fructiferis maturis ca. 5 mm. latis; fructibus maturis rubris vel roseis, 2.5–3.5 cm. latis. HOLOTYPUS: *Streimann & Stevens LAE 53863* (CANB).

DISTRIBUTION. Papua New Guinea; primary and regrowth rain forests; 600–2400 meters.

Papua New Guinea. WESTERN HIGHLANDS DISTRICT: Lufamunda, 1.6 km. NW of Wabag, *Flenley ANU 2035* (CANB); Hagen-Ogelbeng Road, *Robbins 121* (CANB). MADANG DISTRICT: Domainde, *Henty & Sayers NGF 20581* (BRI). EASTERN HIGHLANDS DISTRICT: northeast slopes of Mt. Michael, *Womersley NGF 11709* (BRI); upper Bena Bena Valley, Namaro Forest, *Robbins 1259* (CANB); Wanatabi, 24 km. S of Okapa, *Womersley NGF 17637* (BRI); Noreikora, *Wheeler ANU 5674* (CANB), *ANU 5674A* (CANB); vicinity of Kainantu, behind Nemuka, *Sayers 166* (BRI, CANB); Aiyura Range, *Womersley NGF 3373* (BRI); 1.6 km. W of Akuna, *Hartley 12129* (CANB); Kassam Pass, *Henty & Coode NGF 29200* (BRI), *Womersley & Vandenberg NGF 37413* (BRI, CANB). MOROBE DISTRICT: vicinity of Aseki, *Stevens LAE 54762* (CANB), *Streimann & Stevens LAE 53863* (CANB, holotype), *LAE 53878* (CANB), *LAE 53958* (CANB); Tymne-Wagau Track, *Hartley 11412* (BRI, CANB); Wagau, *Womersley NGF 17864* (BRI, CANB), *Millar NGF 23422* (BRI, CANB); Partep, *Commonwealth Nutrition Survey NSP 45* (CANB); Bulolo, Hump Logging Area, *Streimann NGF 27772* (BRI); Wau-Edie Creek Area, *Frodin & Hill NGF 26383* (BRI, CANB), *Hartley 11716* (CANB), *Henty NGF 16509* (BRI, CANB), *Millar NGF 23065* (BRI), *Womersley NGF 15272* (BRI, CANB), *Womersley & Brass NGF 11015* (BRI); Lake Trist, *Henty NGF 29026* (CANB). SOUTHERN HIGHLANDS DISTRICT: Mt. Ilu, *Gebo UPNG 1662* (CANB); Mabaria Area, below Agunali near Telabo, *Powell UPNG 1622* (CANB); near Habono Resthouse, 10.4 km. W of Mt. Ne, *Frodin NGF 28468* (BRI, CANB); Mendi Valley, above Kiburu, *Schodde 1316* (CANB). **Cultivated.** PAPUA NEW GUINEA: Western Highlands District, Upper Kaugel Valley, Kepaka, Suwake Pena, planted ornamental, *Bowers 483* (CANB).

In their comparatively large flower size, *Acmena montana* and *A. sorongensis* stand apart from the other Papuasian species of the genus. Whether or not this is an indication that they are closely related, we do not know. There are rather strong leaf differences between the two, given in the keys to the species, and the fruits of the former are somewhat larger than those of the latter.

6. Acmena sorongensis Hartley & Craven, sp. nov.

Arbor parva usque ca. 3 m. alta vel frutex; ramulis glabris, teretibus vel compressis, 3–4 mm. latis; foliis glabris; petiolo ca. 10 mm. longo, 2–4 mm. lato; lamina coriacea, in sicco (praesertim supra) brunneola et plus minusve nitida, lanceolata, 20–45 cm. longa, 4.5–11 cm. lata, basi rotundata vel acuta, apice acuminata, venis primariis utrinsecus costa 12–16, subtus prominentibus; inflorescentiis terminalibus et ex axillis foliatis superioribus orientibus, usque ca. 12 cm. longis, glabris; floribus albis; tubo calycis 6–7 mm. longo, basi stipitato (stipite 1–2 mm. longo), apice 3.5–4 mm. lato; lobis calycis ca. 0.5 mm. altis; petalis orbicularibus, ca. 2 mm. latis; staminibus 1–2 mm. longis; pedicellis fructiferis maturis ca. 1.5 mm. latis; fructibus maturis rubris, ca. 2 cm. latis. HOLOTYPUS: *van Royen 3195* (CANB).

DISTRIBUTION. Irian Jaya, Vogelkop Peninsula in the vicinity of Sorong; primary rain forests at about 60 meters.

Irian Jaya. VOGELKOP PENINSULA: hills S of the town of Sorong, *van Royen 3334* (CANB); Klabala River SE of Sorong, *van Royen 3195* (CANB, holotype), *3207* (CANB).

Acmena sorongensis is possibly most closely related to *A. montana* (see under that species).

7. Acmena triphlebia (Diels) Hartley & Craven, comb. nov.

Syzygium triphlebium Diels, Bot. Jahrb. **57**: 400. 1922. TYPE: *Ledermann 10288*, Northeast New Guinea, Sepik District, Lordberg.

Small to large tree to about 20 m.; branchlets glabrous, with bark tending to crack and flake off, terete or compressed, 3–5 mm. wide. Leaves glabrous; petiole (5–)10–15 mm. long, 1–2 mm. wide; leaf blade subcoriaceous to coriaceous, drying brownish, rarely somewhat glossy above, narrowly to broadly elliptic to lanceolate, 12–17(–22) cm. long, 3–4.5 (–7) cm. wide, base rounded to acute, apex acuminate, veins rather prominent, conspicuously paler than the brownish leaf blade surface, main veins about 10 on each side of the midrib. Inflorescences terminal and from the axils of the upper leaves, to about 15 cm. long, glabrous. Flowers white or cream; calyx tube 2.5–3 mm. long, at the base narrowed into a stipe 1–1.5 mm. long, at the apex 2–2.5 mm. wide; calyx lobes about 0.5 mm. high; petals orbicular, about 1 mm. wide; stamens 0.5–1 mm. long. Mature fruiting pedicels about 1 mm. wide; mature fruits white or cream, about 1 cm. wide.

DISTRIBUTION. Irian Jaya, Papua New Guinea; primary and regrowth rain forests; 60–2000 meters.

Irian Jaya. Hollandia, *Kostermans & Soegeng 134* (L). **Papua New Guinea.** SEPIK DISTRICT: Amanab-Kamberatore Road, *Streimann & Martin LAE 52840* (CANB), Lordberg, *Ledermann 10288* (L, isotype of *Syzygium triphlebium* Diels). WESTERN HIGHLANDS DISTRICT: Pokaris, near Kompiam, *Flenley ANU 2872* (CANB). MOROBE DISTRICT: Markham Point, about 11.2 km. W of Lae, *Hartley 10066* (CANB), Upper Watut River, *Havel & Kongara NGF 17289* (BRI, CANB); Edie Creek Road about 6.4 km. SW of Wau, *Hartley 11971* (BRI, CANB). SOUTHERN HIGHLANDS DISTRICT: near Hedamari Mission, *Powell UPNG 2401* (CANB); Lake Kutubu, near Tage, *Schodde 2244* (CANB).

This plant has anthers and seeds that are characteristic of *Acmena* rather than of *Syzygium*, where it was placed originally by Diels and later by Hartley and Perry (1973). The isotype cited above is in bud and is too young to determine the manner of anther dehiscence. The specimen is otherwise a good match, however, for the other collections cited, of which three are in flower and two are in fruit.

Acmena triphlebia is readily distinguishable from the other Papuasian species of the genus by the conspicuously pale veins of its leaves. Its closest relative may be *A. dispansa* (see under that species).

Excluded Species

Syzygium acmenoides Merr. & Perry, Jour. Arnold Arb. 23: 291. 1942. As is noted above, this species was informally referred to *Acmena* by Hartley and Perry (1973: 220). We have examined an isotype and a paratype — *Brass 8644*, Papua, Western District, Wassi Kussa River, Tarara (BRI, isotype), and *Brass 8465*, Papua, Western District, Penzara, between Morehead and Wassi Kussa Rivers (BRI, paratype) — and have found that they are, in fact, correctly placed in *Syzygium*. Both specimens are in fruit, and the seeds do not have the intercotyledonary placental material characteristic of *Acmena*. Also, we have found a single stamen remaining on one of the fruits of the paratype, with anther sacs of *Syzygium* (i.e., elongate, parallel, and laterally dehiscent by a longitudinal slit).

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Merrill, E. D., & L. M. Perry. A synopsis of *Acmena* DC., a valid genus of the Myrtaceae. Jour. Arnold Arb. **19**: 1–20. 1938.

——— & ———. Plantae Papuanae Archboldianae, IX. Jour. Arnold Arb. **23**: 233–297. 1942. [*Acmena*: pp. 247, 248.]

Schmid, R. Floral anatomy of Myrtaceae. I. *Syzygium*. Bot. Jahrb. **92**: 433–489. 1972.

INDEX TO EXSICCATAE

The numbers in parentheses refer to the corresponding species in the text.

Bowers *483* (5).

Brass *675* (1); *7766*, *7941* (4); *7977* (1); *8283* (4); *28857* (3).

Brass & Versteegh *11131* (aff. 1); *11142* (1).

Carr *14505*, *15880* (1).

Clemens *8233A* (1).

Commonwealth Nutrition Survey *NSP 45* (5).

Craven & Schodde *269* (1); *1245* (aff. 1).

Flenley *ANU 2035* (5); *ANU 2872* (7).

Floyd *NGF 6553* (1).

Frodin *NGF 26838*, *NGF 26696* (1); *NGF 28468* (5).

Frodin & Hill *NGF 26383* (5).

Gebo *UPNG 1662* (5).

Hartley *10040*, *10117*, *10134* (1); *10966* (7); *11000*, *11025* (1); *11412* (5); *11444* (1); *11510*, *11710* (5); *11971* (7); *12129* (5); *12388* (1).

Havel & Kongara *NGF 17289* (7); *NGF 17322* (1).

Henty *NGF 12416*, *NGF 14369* (1); *NGF 16509* (5); *NGF 28095* (1); *NGF 29026* (5); *NGF 38613* (1).

Henty & Coode *NGF 29200* (5).

Henty & Foreman *NGF 42662* (aff. 1).

Henty & Sayers *NGF 20581* (5).

Hoogland & Craven *10177* (1).

Kajewski *2353* (1).

Kalkman *BW 3443* (1); *BW 6372* (aff. 1).

Katik *NGF 46699* (1).

Kokkelink *BW 2293* (1).

Kostermans & Soegeng *134* (7).
Ledermann *10288* (7).
Lelean *NGF 46390* (1).
Millar *NGF 12283* (1); *NGF 23065*, *NGF 23422* (5).
Paijmans *349*, *389* (4).
Powell *UPNG 1622* (5); *UPNG 2401* (7).
Pullen *5677* (1); *7147* (4).
Ridsdale *NGF 30528* (1).
Ridsdale & Galore *NGF 33712*, *NGF 33718* (4).
Robbins *121*, *1259* (5).
van Royen *3195*, *3207*, *3334* (6).
Sayers *166* (5).
Schodde *1316* (5); *1539* (1); *2244* (7); *2607*, *5356* (1).
Schodde & Craven *3964* (1).
van der Sijde *BW 4001* (1).
Stevens *LAE 54762* (5).
Streimann *NGF 24081* (1); *NGF 27772* (5).
Streimann & Kairo *NGF 39397* (aff. 1); *NGF 47718*, *LAE 51516* (1).
Streimann & Martin *LAE 52840* (7).
Streimann & Stevens *LAE 53863*, *LAE 53878*, *LAE 53958* (5).
Waterhouse *128–B*, *475–B* (1).
Wheeler *ANU 5674*, *ANU 5674A* (5).
Womersley *NGF 3373*, *NGF 11709*, *NGF 15272*, *NGF 17637*, *NGF 17864* (5); *NGF 24926* (aff. 1); *NGF 43722*, *NGF 46426* (1).
Womersley & Brass *NGF 11015* (5).
Womersley & Havel *NGF 17710* (4).
Womersley & Vandenberg *NGF 37413* (5).

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TWO NEW SPECIES OF EUPHORBIA SUBGENUS AGALOMA FROM MEXICO

WILLIAM R. BUCK AND MICHAEL J. HUFT

THE SUBGENUS AGALOMA (Raf.) House of Euphorbia L. comprising perhaps one hundred and fifty species in the New World (and one in southern Africa), is taxonomically complex and poorly understood. When Boissier revised the genus in 1862, he distributed among ten sections the seventy-seven species of subg. AGALOMA known to him. As more and more species were described, the distinctions between many of the sections became less clear, and today subg. AGALOMA stands in need of thorough revision. In the course of preliminary numerical studies of the subgenus carried out by the junior author, many unidentified specimens, including several undescribed species, were found in the larger American herbaria.

We now describe two of these species from Mexico as new.

Euphorbia arteagae Buck & Huft, sp. nov. FIGURE 1.

Frutex ad 1 m. altus ramosissimus. Ramificatio ternata et divaricata. Rami ramulique glabri, teretes; rami juniores virides, vetustiores cortice exarato, rubello; rami ultimi spiniformes. Folia non visa, ut videtur ternata, decidua; cicatrices foliorum 1.35–1.9 mm. latae, 0.7–1 mm. altae. Cyathia pedunculata, solitaria vel bina ternaque aggregata, infundibuliformia, villosa, orificio ca. 2.5 mm. diametro; pedunculus ca. 0.75 mm. longus, puberulus, prope basin aliquot rudimentis instructus; lobi 6, albi, laciniati, ca. 2 mm. longi; glandulae 6, ellipticae, 1.6–1.85 mm. longae, 0.75–1.1 mm. latae, virides, in sicco flavescentes; appendices petaloideae albae, 6, suborbiculatae, 2.5–3.2 mm. longae, 2.2–2.75 mm. latae, erosae, supra glabrae, infra sparsim villosae. Flores masculi ca. 60. Bracteolae inter flores masculos numerosae, albae, plumosae, 2.5–2.75 mm. longae. Flores feminei 1; styli 3, ca. 1 mm. longi, basi uniti, pro $\frac{1}{3}$–$\frac{1}{2}$ longitudine furcati; stigmata subcapitata. Capsula subglobosa, trisulcata, apice leviter depressa, glabra, brunnea, ca. 6 mm. diametro. Semina ovoidea, ca. 4 mm. diametro, rubiginosa, tuberculata, ecarunculata.

TYPE. Mexico, Michoacán: between Río Tepalcatepec and Arteaga, ca. 75 km. north of Arteaga, along the highway south from "Cuatro Caminos" (3 km. south of Nueva Italia and 30 km. east of Apatzingán) in rocky ravine, elevation 350 m., with *Pseudosmodingium*, 24 February 1965, *Rogers McVaugh 22525* (holotype, MICH; isotypes to be distributed).

Euphorbia arteagae clearly belongs to section ALECTOROCTONUM (Schlechtendal) Boissier, one of the sections recognized by Boissier that still appears to be distinct and well defined. With the other members of the section, it shares a shrubby habit, ternate branching, numerous plumose bracteoles between the male flowers, styles that are united at the base

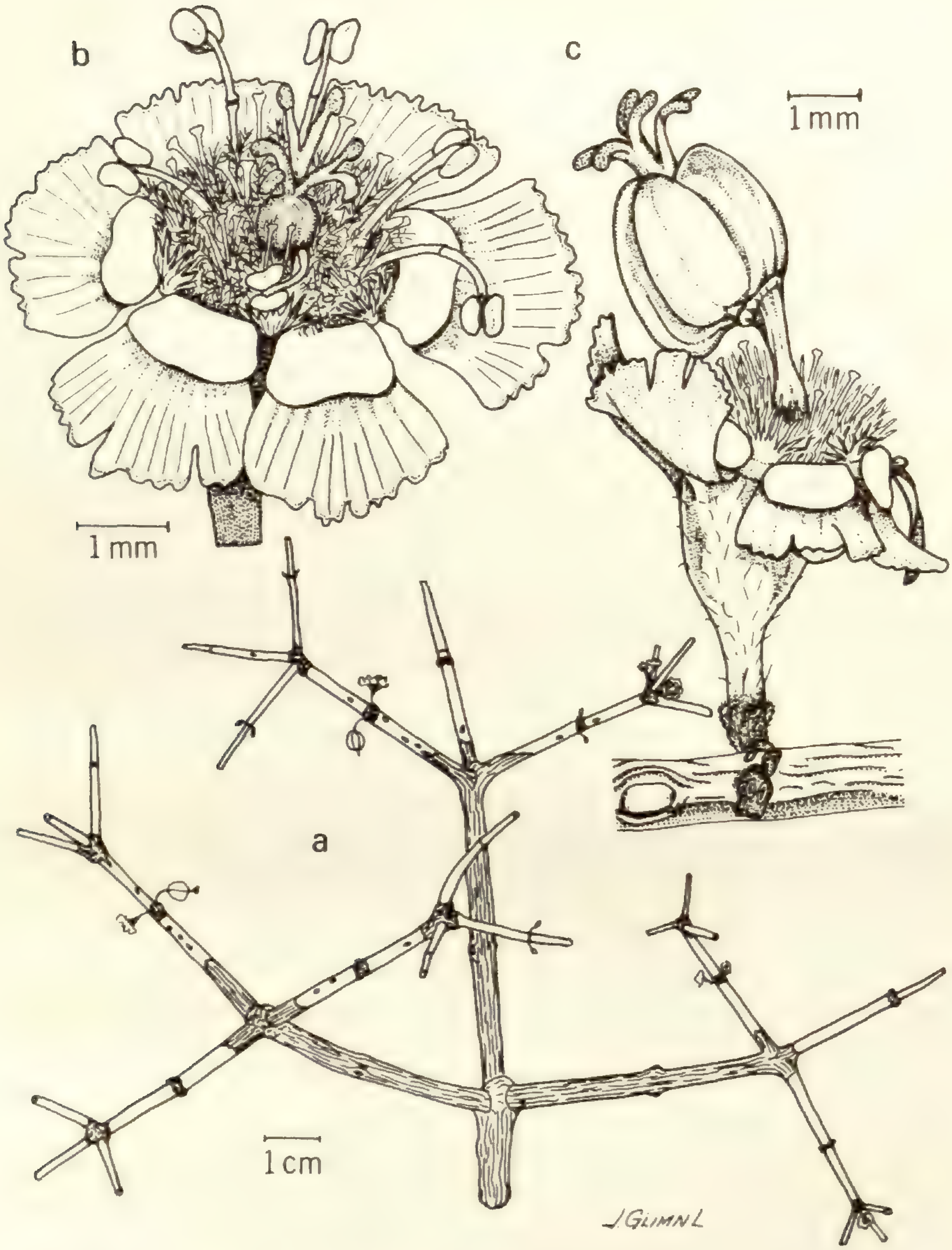

FIGURE 1. **Euphorbia arteagae** (*McVaugh 22525*, MICH): a, flowering branch; b, cyathium with immature capsule, top view; c, cyathium with mature capsule, side view.

and bifid one-third to one-half their length, and irregularly tuberculate seeds. It may be distinguished from all other members of sect. ALECTOROCTONUM, indeed from all other members of subg. AGALOMA, by the presence of six glands on the cyathium, rather than five or fewer. The reduced inflorescence, the divaricate branching, and the thornlike ultimate branchlets of this species are also unique in sect. ALECTOROCTONUM. Although some members of the section TRICHOSTERIGMA (Klotsch & Garcke) Boissier (e.g., *E. misera* Bentham and *E. californica* Bentham) are shrubby and exhibit divaricate branching, nothing else seems to indicate a close relationship of *E. arteagae* to that section. The presence of stubs below the cyathium (FIGURE 1c) suggests that the inflorescence is reduced and that *E. arteagae* may be an advanced member of its section.

Several other species of sect. ALECTOROCTONUM, such as *E. ligustrina* Boissier and *E. nudiflora* Jacq., are occasionally collected without leaves at flowering time, but since other collections of these species are sometimes seen with leaves and flowers appearing simultaneously, we hesitate to state, on the basis of one collection, that the absence of leaves at flowering time is characteristic of *E. arteagae*.

Euphorbia guiengola Buck & Huft, sp. nov. FIGURE 2.

Frutex ca. 1 m. altus, sparsim ramosus. Caules expansi vel ascendentes, virides, teretes, paene glabri autem pilis paucis albis multicellularibus. Folia alterna; stipulae glanduliformes; lamina ovata 1.7–5.7 cm. longa, 1.2–4.1 cm. lata, ca. 1.5-plo longior quam latior, integra, supra glabra, infra glauca et sparsim pubescens pilis multicellularibus uniseriatis 2–3 mm. longis, margine ciliis 0.5–1 mm. longis referta; petiolus 4–6 mm. longus, dense pubescens pilis multicellularibus uniseriatus 0.5–1 mm. longis. Inflorescentiae laterales atque terminales, ascendentes, ca. 5 cm. longae, 1–4-plo dichotomae, cyathiis 1–15, ramis viridibus teretibus 0.1–0.4 mm. diametro dense pubescentibus. Bracteae oppositae; lamina lanceolata (–ovata), acuta, 2.3–3(–7) mm. longa, 1–1.2 mm. lata, 2.5–3-plo longior quam latior, integra, supra glabra, infra sparsim pubescens pilis 0.5–1 mm. longis, margine ciliis 0.5–1 mm. longis referta; petiolus dense pubescens, 0.5–1 mm. longus. Cyathia rubiginosa, obconica, 1 mm. alta, villosa pilis expansis incoloratis, orificio ca. 2 mm. diametro; pedunculus glanduloso-pilosulus, 0.6–1.2 cm. longus, ca. 0.6 mm. diametro; lobi 5, obovati, albi vel interdum versus apicem purpurei, erecti, ca. 1.5 mm. longi, ca. 1.25 mm. lati, laciniati vel erosi; glandulae 5, luteae vel interdum purpureae, ellipticae, ca. 0.9 mm. longae, 0.5 mm. latae, crenulatae, appendices petaloideae flabellatae, 2–2.7 mm. longae, apice 1.8–2.5 mm. latae, erosulatae vel integrae, glabrae, omnes albae vel e basi ad supra medium atropurpureae apice albae. Flores masculi ca. 25. Bracteolae inter flores masculos obsoletae. Flores feminei 1; styli 3, ca. 1 mm. longi, profunde furcati, basi libri; stigmata subcapitata. Capsula 2–3 mm. diametro, subglobosa, trisulcata, apice leviter depressa, glabra, brunnea punctis parvis albis obsitis. Semina ovoidea, ecarunculata, 1–1.5 mm. longa, 0.6–0.8 mm. diametro, rubro-aurantiaca, obtusa triangula, foveolato-tuberculata.

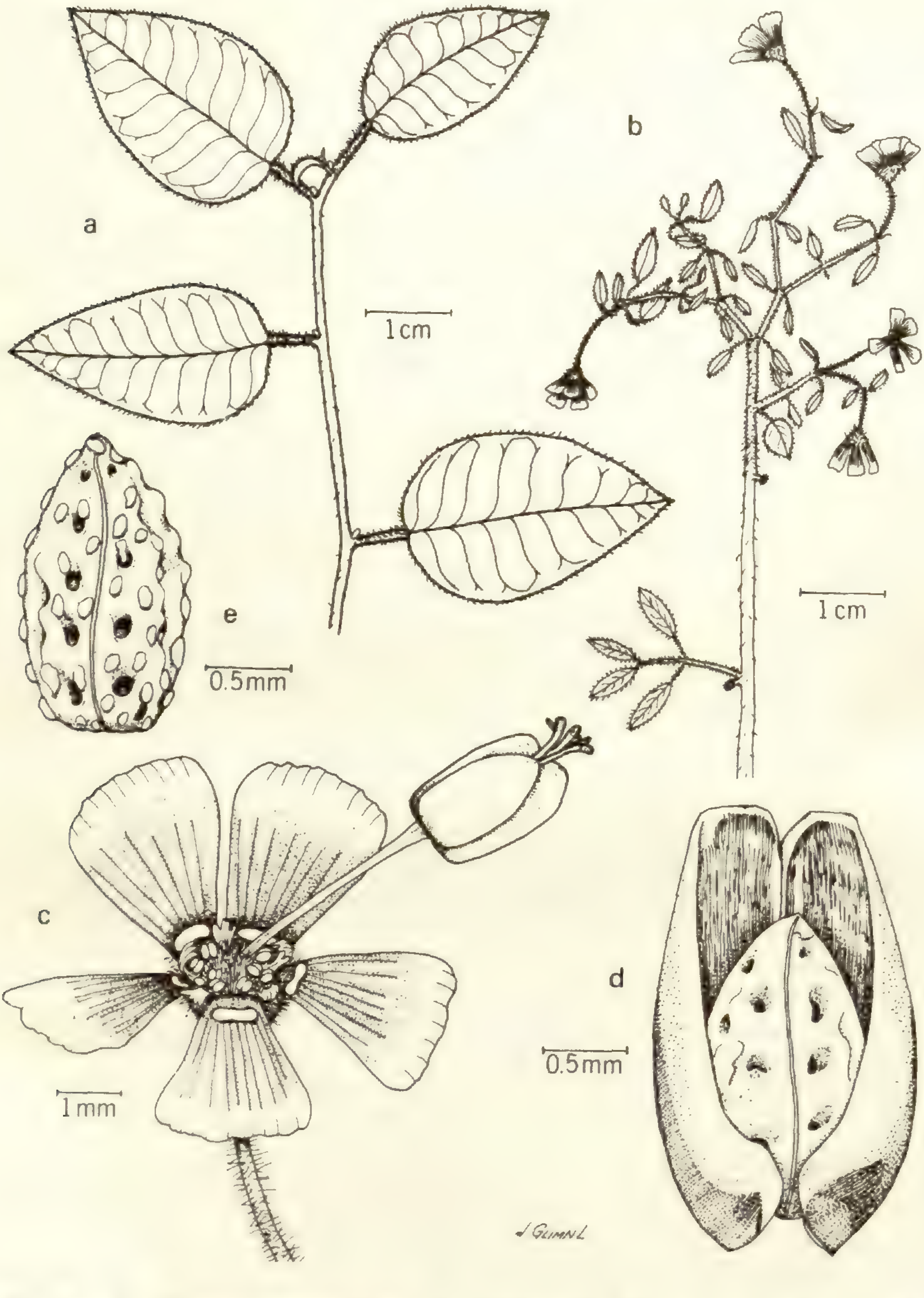

FIGURE 2. **Euphorbia guiengola**: a, vegetative branch (*MacDougall*, US 2536478); b, terminal inflorescence (*MacDougall*, US 2549630); c, cyathium with mature capsule (*MacDougall*, US 2549630); d, seed surrounded by a portion of the capsule (*MacDougall*, US 2586633A); e, seed (*MacDougall*, US 2586633A).

TYPE. Mexico, Oaxaca: Tehuantepec, lower slopes of Cerro Guiengola, elev. approx. 500 feet, 14 October 1965, *T. MacDougall s.n.* (holotype, US; isotype, MICH).

ADDITIONAL SPECIMENS. **Mexico.** CHIAPAS: Rizo de Oro, Cintalapa, 19 November 1966, *T. MacDougall s.n.* (MICH, US). OAXACA: Río Hondo, San Carlos Yautepec, 13 February 1962, *T. MacDougall s.n.* (US 2364780); Cerro Guiengola, 15 January 1896, *Caec. et Ed. Seler 1611* (GH); 27 August 1966, *T. MacDougall s.n.* (US); material cultivated at the University of California Botanical Garden, Berkeley, original material from Cerro Guiengola collected by T. MacDougall, prepared 17 July 1960, Botanical Garden accession no. 59.608 (US 2369899); prepared 24 May 1962, accession no. 58.856–1 (US 2384286 and 2549630); prepared 8 August 1968, accession no. 58.856 (US 2536478).

The position of *Euphorbia guiengola* within subg. AGALOMA is not as easy to determine as is that of *E. arteagae*. It would appear to belong to sect. CYTTAROSPERMUM Boissier on the basis of its alternate leaves, opposite reduced bracts, absence of bracteoles between the staminate flowers, and styles that are free at the base and deeply bifurcate. The numerical studies mentioned above, however, indicate that this section, a large and diffuse group most abundant in Mexico and Central America, is probably not a natural group.

Euphorbia guiengola most closely resembles the Guatemalan species *E. ephedromorpha* Bartlett, with which it shares a shrubby habit, prostrate or ascending zig-zag stems, sparse branching, ovate leaves with silvery-white undersides, compact lateral and terminal inflorescences that are densely glandular-pilose, and obconical cyathia. The two species can be distinguished by means of the following key:

Stems winged; petaloid appendages oblong or spatulate. . . *E. ephedromorpha.*
Stems terete, not winged; petaloid appendages flabellate. . . . . *E. guiengola.*

Bartlett (1911) described the section EPHEDROMORPHA to accommodate *E. ephedromorpha* and stated that a second species of the section "represented in the Gray Herbarium by fragments too poor to serve as a type, was collected at Cerro Quiengola [*sic*], Oaxaca, Mexico, *Caec. & Ed. Seler 1611.*" We have examined these specimens, and they appear to us to be identical with *E. guiengola*. Owing to the confusion in the classification of subg. AGALOMA, we hesitate to assign *E. guiengola* to a definite section until further studies of the subgenus can be carried out.

ACKNOWLEDGMENTS

This paper developed from a project completed by the senior author for a class in advanced systematics taught by Dr. Rogers McVaugh at the University of Michigan in the winter of 1974. We wish to express our gratitude to Dr. McVaugh for his assistance and advice, and for reading the manuscript. The material of *E. guiengola* was being studied by C. V. Morton of the United States National Museum at the time of his death in 1972. It was made available to us via Dr. McVaugh through the

courtesy of Dr. Velva E. Rudd of the National Museum. We are also indebted to Janice Glimn Lacy for making the drawings.

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COVER: The conelike follicetum or fruit aggregate of *Magnolia tripetala* L., an American species of section Rhytidospermum Spach, is the basis for our new cover design. Individual follicles of the fruiting body were used in the devices for other parts of the Journal and for the offprints. The designs were all drawn by Karen S. Velmure, who also planned and prepared the three preceding covers for the Journal, as well as the accompanying devices.

The section Rhytidospermum, of which *Magnolia tripetala* is the type, includes three species of Asia and four to six of America. These are large shrubs or deciduous trees with leaves crowded into false whorls at the end of branchlets, alternate and widely spaced on new shoots. *Magnolia tripetala*, the umbrella-tree or elkwood, is native in rich woods of eastern North America from southern Pennsylvania and West Virginia, south into Florida, and westward through Ohio and Kentucky to Arkansas and Missouri. It is sometimes found escaped from cultivation north into central Massachusetts. In cultivation it has been involved in many hybrid combinations.

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THE GENUS MASTIXIODENDRON (RUBIACEAE)

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ALTHOUGH THEY COMPRISE one of the largest angiosperm families, members of the Rubiaceae are remarkably uniform in a number of characters. The principal characters shared by nearly all Rubiaceae include opposite, stipulate, simple, entire leaves; inferior ovaries; and sympetalous corollas with the stamens equaling the corolla lobes in number and inserted alternately with them. Because the family is so easily characterized, taxa which vary from the accepted "norm" are particularly conspicuous. Bremekamp (1966) has pointed out that, although a few genera (e.g., *Gaertnera* Lam. and *Pagamea* Aublet) may possess ovaries which are wholly or partly superior at some stage in their ontogeny, they nonetheless agree with the Rubiaceae in other characters and should be included within that family. Bremekamp rightly cautions that the importance of the inferior ovary (like any other single character) is not to be overrated in determining the limits of the Rubiaceae. Similarly, there are a few Rubiaceae with polypetalous corollas (e.g., *Hedstromia* A. C. Sm.), probably resulting from a progressive shortening of the corolla tube. With regard to other, less diagnostic features, the list of exceptions could be extended considerably.

An especially aberrant genus, but one rarely mentioned as such in the literature, is *Mastixiodendron* Melchior. Its polypetalous corollas and, in at least a few species, its semisuperior ovaries have persistently drawn attention away from other, more recondite features which label the genus as definitely rubiaceous. At various times associated with the Loganiaceae or the Cornaceae, there seems now to be little doubt that *Mastixiodendron* ought to be counted among the Rubiaceae, even though a few of its salient morphological characters might seem anomalous in that family.

HISTORY

The genus *Mastixiodendron* was first described by Melchior (1925) to accommodate *Fagraea pachyclados* K. Schum., a species from New Guinea, described in the Loganiaceae. Primarily on account of its polypetalous corollas, Melchior aligned *Mastixiodendron* with *Mastixia* Blume of the Cornaceae. He was evidently unaware that the transfer of *F. pachyclados*

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to the Cornaceae had earlier been suggested by Gilg and Schlechter (in Gilg & Benedict, 1916, p. 197), although *Fagraeopsis*, the generic name which they proposed, was a provisional name. Melchoir described the morphology and anatomy of *Mastixiodendron* in some detail, enumerating the characters by which it differs from other Cornaceae.

Gillespie (1933) described *Dorisia rarissima* as a new genus and species of Cornaceae from Fiji. He noted a close similarity among *Dorisia*, *Mastixia*, and *Mastixiodendron*, the first genus being distinct in its almost entirely inferior ovaries. A few years later, *Dorisia* was reinvestigated by Smith (1936, p. 140), who, in spite of its separate corolla lobes, regarded the genus as entirely rubiaceous in its vegetative characters. With supporting evidence from wood anatomy and stomatal structure, he removed *Dorisia* from the Cornaceae and placed it in the tribe Chiococceae of the Rubiaceae.

Danser (1934, p. 69) was the first author to suggest that the New Guinean species of *Mastixiodendron* be transferred from the Cornaceae to the Rubiaceae, an alignment suggested to him by the large, imbricate stipules which are otherwise unknown in the former family. On the basis of leaf and stem structure, Merrill and Perry (1942, p. 416) independently reached the same conclusion and reiterated the close similarity between *Mastixiodendron* and *Dorisia*.

The union of *Dorisia* with *Mastixiodendron* was effected by Smith (1945, p. 108), who, at the same time, added another Fijian species, *M. pilosum*. Soon after, Merrill and Perry (1945, p. 254) described two additional species, *M. smithii*, from New Guinea, and *M. stoddardii*, from the Solomon Islands. A sixth species, *M. robustum*, from Fiji, was later described by Smith (1969, p. 390).

GEOGRAPHICAL DISTRIBUTION

As interpreted here, *Mastixiodendron* includes seven species: *M. pachyclados*, distributed from the Moluccas eastward through New Guinea and the Bismarck Archipelago; *M. smithii* and *M. plectocarpum*, in New Guinea; *M. stoddardii*, in the Bismarck Archipelago and the Solomon Islands; and *M. flavidum*, *M. pilosum*, and *M. robustum*, all endemic to to Fiji. The genus has a distributional pattern which, common among flowering plants of the western Pacific (Smith, 1955), is termed "East Malesian" by van Balgooy (1971).

MORPHOLOGY

HABIT AND DURATION. All species of *Mastixiodendron* are woody; many are large forest trees, while others (*M. flavidum*) are slender trees or large shrubs. The crowns of the arborescent species are variable, but are usually small, dense, and rounded, with heavy, ascending limbs. In some species (*M. smithii*, *M. stoddardii*), the bole is frequently poorly formed.

BARK AND WOOD. Where field notes are available (mostly for collections from New Guinea), the outer bark is described as "pustular" or "flaking," often being shed as relatively large, papery pieces. Such features may be of value in the field identification of the genus. The wood of *Mastixiodendron* is usually described as being hard; it is white to pale brown in color, although darkening on exposure.

The wood anatomy of the genus is reasonably uniform. The vessels are occasionally solitary, but are more often radially aligned in groups of as many as five, rarely more, and with more than 40 vessels per square millimeter of cross sectional area. The vessel elements have simple perforations and diameters from 0.05 mm. (branchlet of *M. pachyclados*, *Brass & Versteegh 13548*) to 0.13 mm. (*M. stoddardii*, *Stoddard 12*). Wood fibers are conspicuously septate, and the pits are generally confined to the radial walls. The rays are multiseriate, heterogeneous, up to four cells wide (*M. stoddardii*), and variable in height from 0.4 mm. (*M. flavidum*, *A. C. Smith 1932*) to 1.25 mm. (*M. stoddardii*); extended uniseriate wings or sheath cells are absent. Axial parenchyma is also absent.

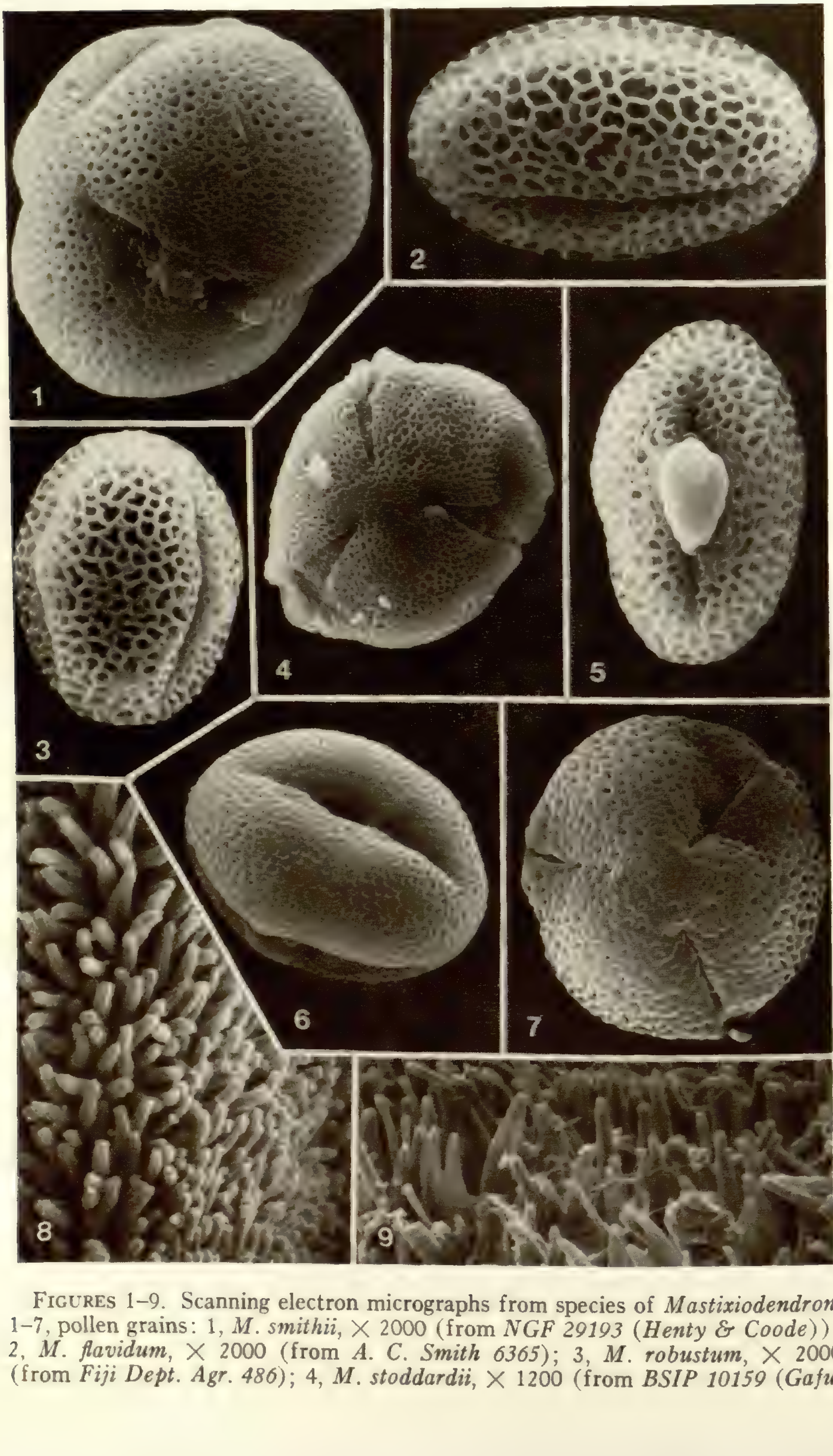
HAIRS. Trichomes of various size are always present on the inner surfaces of the corolla lobes. The corolla hairs are unicellular, as is usual in the Rubiaceae, and have smooth to somewhat striate walls. Minute hairs are also present on other inflorescence and flower parts. Only *Mastixiodendron pachyclados* var. *tomentosum* and *M. pilosum* have significant indument on their vegetative parts; epidermal hairs (FIGURES 10, i; 14, f) from their leaf blades have smooth to finely striate and frequently thick outer walls (especially in *M. pilosum*). The lumina of the longer hairs are traversed by as many as ten thin septa.

CRYSTALS. I have observed crystal sand in leaf tissues. Raphides are absent.

LEAVES AND STIPULES. The simple, entire leaves of *Mastixiodendron* are opposite at each node. The leaf blades are coriaceous (thickly so in *M. robustum*) to chartaceous (*M. stoddardii* and *M. pilosum*). The secondary nerves are usually fewer than 15 on each side of the costa, except in *M. plectocarpum* and *M. robustum*, where there are frequently as many as 20 (in the former species they are prominulous above and beneath and often hardly discernible from the tertiary nerves). The stomata (FIGURE 14, a), restricted to the lower surfaces of the leaf blades and much crowded, are paracytic, although the narrow accessory cells are often difficult to see.

The petioles of *Mastixiodendron pachyclados* have a vascular pattern common for the Rubiaceae, consisting of a median strand appearing in cross section as a deep arc with its ends strongly incurved around four "medullary" strands; a number of "accessory" strands are located toward the petiole wings (*Brass 14097*).

The imbricate, interpetiolar stipules are prominent in the terminal buds (FIGURE 10, a, b), but soon fall away leaving conspicuous scars. In all species the stipules may be strongly contorted.



FIGURES 1–9. Scanning electron micrographs from species of *Mastixiodendron*. 1–7, pollen grains: 1, *M. smithii*, × 2000 (from *NGF 29193 (Henty & Coode)*); 2, *M. flavidum*, × 2000 (from *A. C. Smith 6365*); 3, *M. robustum*, × 2000 (from *Fiji Dept. Agr. 486*); 4, *M. stoddardii*, × 1200 (from *BSIP 10159 (Gafui*

INFLORESCENCES. The inflorescences of *Mastixiodendron* are axillary thyrses, although there is considerable variation in size, degree of branching, and number of flowers, all characters that may be species-specific. The bracts are similar in all species; there are usually four at the first node (two bracts and two stipules?), but two at the others. Each inflorescence branch terminates in a dichasium (FIGURES 12, c; 13, b; 14, c, h). A pair of small bracts is always present on the axis which supports each of the lateral flowers of the dichasium; in determining the length of the pedicels of these lateral flowers, I have measured only the distance above the bract pair.

COROLLA. The corolla buds of *Mastixiodendron* are usually 4-angled shortly before anthesis and vary in shape from subglobose (*M. pachyclados*, *M. flavidum*, *M. robustum*) to decidedly longer than broad (*M. smithii*, *M. plectocarpum*, *M. pilosum*). At anthesis, the corolla lobes are always entirely free, but vary considerably in size and shape. As stated previously, they are always pubescent to some degree (pilose in most species to papillate in *M. flavidum*) on their inner surfaces, and glabrous to densely puberulent (*M. smithii*) beneath. The lobes are fleshy, and in *M. pachyclados* there are often shallow depressions on the inner surfaces which partially enclose the stamens in bud.

POLLEN. The microspores of *Mastixiodendron* are tricolporate (the colpi and ora well developed). They range in size from 20–25 × 28–33 μm. (*M. smithii*) to 12–15 × 20–23 μm. (*M. robustum*), and in shape from prolate to oblate. The grains are tectate, although those of Papuasian species (FIGURES 1, 4, 6, 7) are tectate-perforate, whereas pollen of the Fijian taxa (FIGURES 2, 3, 5) is semitectate.

GYNOECIUM. The ovaries of *Mastixiodendron* vary from nearly ¾ superior (*M. stoddardii*) to wholly inferior (*M. plectocarpum*). The superior portion of the ovary is here referred to as the "disc," although it is apparently not glandular. The discs are usually glabrous, but are obscurely puberulent in *M. smithii* and *M. plectocarpum* (FIGURES 8, 9). They vary in shape from broad and flat (*M. plectocarpum*), to rounded (*M. pachyclados*, *M. flavidum*, *M. robustum*), to broadly ovoid (*M. stoddardii*), to subconical (*M. smithii*, *M. pilosum*).

FRUITS AND SEEDS. Fruits of *Mastixiodendron* are all drupaceous and indehiscent. They may be mostly superior (*M. stoddardii*), about half superior (e.g., *M. pachyclados*), or inferior (e.g., *M. plectocarpum*), as suggested by the persistent perianth scar. Similarly, the apices vary from sharply pointed (e.g., *M. stoddardii*) to broadly rounded (*M. plectocar-*

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et al.)); 5, *M. pilosum*, × 2000 (from *Fiji Dept. Agr. 17094*); 6, *M. pachyclados* var. *pachyclados*, × 2000 (from *NGF 29673 (Coode & Cropley)*); 7, *M. plectocarpum*, × 2000 (from *BW 13347 (Schram)*). 8, 9, surfaces of floral discs showing trichomes: 8, *M. smithii*, × 260 (from *NGF 29193 (Henty & Coode)*); 9, *M. plectocarpum*, × 260 (from *Pullen 7327*).

pum). The pericarp is also variable. The exocarp is a thin skin, the mesocarp a fleshy (when alive) to firm layer; the endocarp may be hard and bony or woody, or fibrous and conspicuously cancellate. Relatively thin pericarps with bony endocarps characterize fruits of *M. pachyclados* and *M. stoddardii*. The fruits of *M. robustum* are hard and woody; those of *M. smithii*, woody to fibrous and more distinctly cancellate with resin cavities. The fruits of *M. plectocarpum* are very strongly cancellate and fibrous.

The solitary ovules of *Mastixiodendron* are often somewhat compressed and apparently pendulous; a slightly thickened apical funiculus is discernible, but each ovule adheres to the elongate placenta over most of its length (as do the mature seeds). The placenta is variably swollen beneath each ovule and projects from the dissepiment (evidently the "flap" of tissue figured by Gillespie, 1933, for *M. flavidum*).

FAMILIAL RELATIONSHIPS

Although Melchior (1925) associated *Mastixiodendron* with *Mastixia*, he nevertheless pointed out numerous anatomical differences between those genera, particularly the distribution in the stem cortex of collenchyma, stone cells, fibers, and secretory cells. However, he overlooked the narrow accessory cells and the paracytic ("rubiaceous") structure of the stomata of the present genus and failed to realize that the characters of wood anatomy alone exclude *Mastixiodendron* from an alliance with *Mastixia* or the Cornaceae as a whole, a family in which the vessels are almost always solitary and have scalariform perforation plates with many bars (Metcalfe & Chalk, 1950). Danser (1934, p. 69) further emphasized the large interpetiolar stipules of *Mastixiodendron* as a rubiaceous character, the Cornaceae being exstipulate. Significant morphological characters and the bulk of anatomical evidence therefore suggest that *Mastixiodendron*, in spite of its free corolla lobes and partially superior ovaries, be included within the Rubiaceae.

TRIBAL RELATIONSHIPS

The characters which define infrafamilial taxa in the Rubiaceae have been discussed by Verdcourt (1958) and Bremekamp (1966); interested readers should consult those studies for a re-evaluation of the earlier classification schemes. I agree that the characters employed by Verdcourt and Bremekamp (e.g., the presence or absence of raphid crystals, thin-walled multicellular hairs, and seed endosperm) seem to correlate well with the more traditional subfamilial and tribal characters, among which are the number and position of the ovules, the nature of the fruit, the aestivation of the corolla lobes, and the place of attachment of the stamens.

Because it has endospermous seeds, valvate corolla aestivation, and thick-walled septate hairs, but lacks raphid crystals, *Mastixiodendron* is assignable to the subfamily Cinchonoideae Raf. *sensu* Verdcourt (1958).

I have reviewed the tribes placed in that subfamily by Verdcourt, and in the subfamilies other than the raphid-possessing Rubioideae by Bremekamp, but have not found any tribe which matches the characters of *Mastixiodendron* in all respects. The most likely candidates are the Alberteae Hooker f., Vanguerieae Dumort., and Chiococceae Hooker f., all of which have solitary, pendulous ovules. However, the Alberteae have corolla lobes which are contorted in bud, and the Vanguerieae and Chiococceae are characterized by conspicuously swollen stigmas and an "ixoroid" pollen presentation mechanism (Bremekamp, 1966), all characters conspicuously absent in *Mastixiodendron.* In addition, the Vanguerieae all have porate pollen and seem to be a group of closely related genera (Verdcourt, 1958).

When Smith (1936, p. 140) placed *Mastixiodendron* (*Dorisia*) in the Rubiaceae, he assigned the genus to the tribe Chiococceae, indicating a possible relationship with *Hodgkinsonia* F. Mueller, from Australia. In the tribal key provided by Schumann (1891), *Mastixiodendron*, with its solitary, pendulous ovules, and stamens attached at the base of the corolla tube (in this case the tube is absent), easily keys to the Chiococceae. Of the genera placed by Schumann in that tribe, only *Hodgkinsonia* is palaeotropical; the other nine genera occur in the New World and show little similarity to the present genus. *Hodgkinsonia* resembles *Mastixiodendron* in its frequently 4-merous flowers, valvate corolla lobes, short styles, axillary inflorescences, indehiscent fruits, and caducous stipules. However, flowers of the former genus are definitely sympetalous, the corolla is not especially fleshy, the stamens are inserted on the corolla tube, and the inflorescences are umbelliform. The wood of *Hodgkinsonia* resembles that of *Mastixiodendron* in that the vessels are of nearly the same size and occur in radial groups; the rays are also multiseriate, to four cells wide, and heterogeneous, although in the former genus diffuse axial parenchyma is present, the fibers are not septate, and the rays have long, uniseriate wings.

I have little doubt that *Mastixiodendron* belongs to the Rubiaceae subfamily Cinchonoideae. As to tribal position, the genus seems best placed in the Chiococceae. Smith's suggested relationship between *Mastixiodendron* and *Hodgkinsonia* appears unlikely to me, but I cannot offer a more plausible suggestion at this time. As genera of the Rubiaceae are reinvestigated and the tribes become better understood, it is hoped that the relationships of *Mastixiodendron* will become clearer. However, it can presently only be regarded as an anomalous member of the Cinchonoideae.

INTERSPECIFIC RELATIONSHIPS

Because the tribal affiliations of *Mastixiodendron* are uncertain, it is not possible to distinguish between ancestral and derived characters or to regard one species as "primitive" and others as "advanced." Nevertheless, interspecific relationships are discernible. Among the Fijian species, floral, fruit, and vegetative morphology is relatively diverse, although the oc-

currence of a few intermediate (hybrid?) collections indicates that *M. pilosum* and *M. robustum* are each probably closely related to *M. flavidum*. The restriction of semitectate pollen to the same three species (versus tectate-perforate pollen in others) further suggests that the Fijian taxa evolved from one ancestral population.

Among the extra-Fijian species, *Mastixiodendron smithii* and *M. plectocarpum* seem related on the basis of their pubescent discs and corolla exteriors, and their relatively cancellate and resinous fruits, while *M. pachyclados* and *M. stoddardii* share glabrous discs and relatively thin-walled fruits. Other characters are mentioned under the individual species.

TAXONOMY

Mastixiodendron Melch., Bot. Jahrb. **60**: 167. 1925; Danser, Blumea 1: 69. 1934; Merr. & Perry, Jour. Arnold Arb. **25**: 205. 1944; A. C. Sm., Jour. Arnold Arb. **26**: 108. 1945; Merr. & Perry, Jour. Arnold Arb. **26**: 254. 1945; A. C. Sm., Jour. Arnold Arb. **36**: 288. 1955, Pacif. Sci. **23**: 390. 1969.

Fagraeopsis Gilg & Schlechter in Gilg & Benedict, Bot. Jahrb. **54**: 197, *nom. provis.* 1916; Airy Shaw, Wills Dict. Fl. Pl. & Ferns. ed. 7. 443, *nomen nudum*, 1966, ed. 8. 453, *nomen nudum*, 1973.

Dorisia Gillespie, Hooker's Icon. Pl. **32**: *t. 3190.* 1933.

Trees or rarely shrubs, glabrous to pilose with spreading, septate hairs; branchlets compressed when young, at length subterete, ringed by prominent stipule scars; stipules caducous, prominent in terminal buds, strongly imbricate, often dextrorsely contorted, coriaceous to membranaceous at margin, glabrous or occasionally minutely puberulent with scattered hairs; petioles stout to relatively slender; leaf blades coriaceous to chartaceous, ovate to elliptic to broadly obovate, rounded to bluntly cuspidate or acuminate at apex, decurrent on petiole at base, entire at margin, the secondary nerves spreading from costa and anastomosing submarginally; inflorescences variously puberulent, thyrsoid with opposite branches terminating in 3-flowered dichasia, axillary to ultimate or penultimate leaves, the peduncles stout to slender, the inflorescence branches subtended by membranaceous bracts; calyx lobes 4 (very rarely 5), shortly united at base, entire at margin, glabrous outside; corolla lobes 4, fleshy, valvate in bud, free to base, entire at margin, essentially glabrous to finely but densely puberulent outside, papillate to pilose inside; stamens 4, alternate with corolla lobes, the filaments filiform to narrowly subulate, the anthers 2-locular, oblong-ovoid, subbasifixed; ovary 2-locular, somewhat less than half to almost completely inferior, the inferior portion turbinate to subglobose, the superior portion (disc) broad and flat to sharply raised and subconical; ovules solitary and subpendulous in each ovary locule; style often caducous, subcylindrical, glabrous, often shortly divided at apex; fruits drupaceous, woody to fibrous, frequently 1-locular by abortion, crowned or variously ringed by perianth scar; seeds long-ellipsoid, attached

over most of length to dissepiment, the testa variously rugose, the endosperm present.

TYPE SPECIES. *Mastixiodendron pachyclados* (K. Schum.) Melch.

KEY TO THE SPECIES AND VARIETIES OF MASTIXIODENDRON

1. Branchlets commonly more than 6 mm. broad toward apex; leaf blades usually rounded or broadly obtuse or occasionally bluntly cuspidate at apex; inflorescences relatively robust, with 3 to 4 (to 5) orders of branching; fruits subcylindrical to ellipsoid, rarely subglobose or turbinate, ringed by perianth scar 8–15 mm. below apex; Moluccas, New Guinea, and Bismarck Archipelago.
   2. Leaf blades entirely glabrous beneath. ..... 1a. *M. pachyclados* var. *pachyclados.*
   2. Leaf blades pilose to puberulent beneath with scattered, spreading hairs. ..... 1b. *M. pachyclados* var. *tomentosum.*
1. Branchlets commonly less than 6 mm. broad toward apex; leaf blades acuminate to obtuse and bluntly cuspidate at apex, not rounded; inflorescences with up to 3 orders of branching; fruits not as described above.
   3. Corolla lobes densely puberulent outside; disc subconical, finely but densely puberulent to papillate with minute, gray to stramineous hairs; mature fruits more than 45 × 20 mm., ringed by perianth scar less than 10 mm. from usually pointed apex; New Guinea. ..... 2. *M. smithii.*
   3. Corolla lobes glabrous to almost imperceptibly puberulent outside with scattered hairs; disc not as described above; mature fruits either less than 45 mm. long, or with perianth scar more than 10 mm. below apex.
      4. Corolla limb about 10 mm. across; stamens with filaments frequently more than 2.5 mm. long; fruits long-tapering distally, ringed by perianth scar 15–25 mm. below apex; New Britain and Solomon Islands. ..... 3. *M. stoddardii.*
      4. Corolla limb less than 10 mm. across; stamens with filaments up to 2.5 mm. long; fruits not as described above.
         5. Disc broad, flat, densely puberulent toward center, glabrous toward margin; fruits to 30 mm. long, ovoid to obovoid, broadly rounded at apex, the endocarp strongly cancellate and filled with clear to reddish resin; New Guinea. ..... 4. *M. plectocarpum.*
         5. Disc rounded or subconical, glabrous; fruits not as described above; Fiji.
            6. Peduncles 3–4 mm. in diameter; calyx lobes more than 1.5 mm. broad at base; corolla lobes usually more than 2 mm. broad; fruits more than 15 mm. broad, the perianth scar 15–20 mm. below blunt to rounded apex. ..... 5. *M. robustum.*
            6. Peduncles less than 3 mm. in diameter; calyx lobes less than 1.5 mm. broad at base; corolla lobes to 2 mm. broad; fruits less than 15 mm. broad, the perianth scar less than 10 mm. from acute apex.
               7. Leaf blades glabrous beneath, rarely puberulent; flower buds nearly as broad as long; corolla lobes less than 3 mm. long; disc broadly rounded, less than 0.5 mm. high; style less than 1 mm. long. ..... 6. *M. flavidum.*
               7. Leaf blades pilose to tomentulose beneath; flower buds

more than twice as long as broad; corolla lobes 4–4.5 mm. long; disc subconical, about 1.5 mm. high; style 1.5–2 mm. long. ..... 7. *M. pilosum*.

1. Mastixiodendron pachyclados (K. Schum.) Melch., Bot. Jahrb. 60: 168. *t. 1.* 1925.

Tree to 55 m. high, the bole straight, to 31 m. high, to 2 m. d.b.h., the buttresses straight, to 4 m. high, the crown compact to spreading with stout branches; bark variable from dark to pale gray or brown, pustular to fibrous and flaking, the inner bark and wood white to pale brown, darkening on exposure; branchlets robust, 6–10 mm. broad toward apex, dark red-brown to pale gray or brown; mature stipules lanceolate, 20–40 mm. long, 8–12 mm. broad, acuminate at apex; petioles stout, semiterete, (5–)10–30 mm. long, 3–6(–18) mm. broad, winged by base of leaf blade; leaf blades coriaceous, broadly obovate to elliptic, occasionally nearly spathulate, (11–)13–45 cm. long, (6–)8–24 cm. broad, rounded to very bluntly obtuse or occasionally bluntly cuspidate at apex, often strongly revolute at margin, glabrous and glossy above, glabrous or pilose to puberulent beneath with scattered hairs to 0.5 mm. long, the costa plane to canaliculate above, strongly raised and rounded beneath, the secondary nerves 7 to 12 per side, prominulous above, raised and rounded beneath. the tertiary nerves and veinlets prominulous to plane above and beneath; inflorescences puberulent with minute, scattered hairs to 0.1 mm. long, open to congested, with 3 to 4(to 5) orders of branching and 200 to 1000 (rarely more) flowers, 10–22 × 9–24 cm. at anthesis, 12–25 × 12–24 cm. in fruit, about as broad as long, the peduncles subterete, 1–5(–10) cm. long, 3–6 mm. in diameter, the inflorescence bracts deltoid to ovate, to 5 mm. long, 0.5–2.5 mm. broad at base, acute at apex; pedicels relatively stout, 1–1.5(–3) mm. long; calyx limb subpatelliform, spreading, 2.5–3(–4) mm. across, the lobes very broadly deltoid, 0.3–0.6(–0.8) mm. long, 1.5–2 mm. broad at base and united into a shallow cup, rounded to obtuse and minutely apiculate at apex, glabrous to puberulent outside with a few scattered hairs; corolla limb 6–8(–10) mm. across, the lobes yellow-green to greenish white, subdeltoid to broadly ovate, 2.5–3.5 mm. long, (1.5–)2–3(–3.5) mm. broad, glabrous to finely puberulent outside with scattered, minute, stramineous hairs, pilose distally inside with stiff, yellow hairs to 0.8 mm. long, glabrous toward base; filaments of stamens 1.5–3 mm. long, to 0.5 mm. broad at base, tapering toward apex, the anthers 0.8–1 × 0.5 mm.; inferior portion of ovary to 1 mm. long, 1.5–2.5 mm. in diameter, the disc broad and flat to rounded, about 0.5 mm. high, glabrous; style 1–1.5 mm. long, about 0.2 mm. in diameter, truncate to divided to 0.5 mm. at apex; fruits hard, yellow to green, drying pale gray or brown to black, glabrous, usually subcylindrical to ellipsoid, occasionally subglobose to broadly ovoid, rounded or bluntly pointed at both ends, (15–)22–35 × 8–15 mm., ringed by perianth scar 5–13 mm. below apex, the mesocarp dense, 0.5–1(–4) mm. thick, the endocarp to 3 mm. thick, bony; seeds 12–20 × 4–5 mm., pale yellow-brown, often folded lengthwise when dry.

Having examined nearly all of the available collections of *Mastixiodendron pachyclados*, I have distinguished two varieties based on the indument characters outlined in the preceding key. The vast majority of the collections are referable to the typical variety in which the leaf blades have glabrous lower surfaces. Specimens with pubescent leaf blades constitute *M. pachyclados* var. *tomentosum*.

1a. Mastixiodendron pachyclados (K. Schum.) Melch. var. **pachyclados.** FIGURES 6; 10, a–h.

Fagraea pachyclados K. Schum. in K. Schum. & Lauterb., Nachtr. Fl. Deutsch. Schutzgeb. Südsee, 349. 1905; Gilg & Benedict, Bot. Jahrb. **54:** 196. 1916.
Mastixiodendron pachyclados Melch., Bot. Jahrb. **60:** 168. *t. 1.* 1925; C. T. White, Jour. Arnold Arb. **10:** 257. 1929; Lauterb., Bot. Jahrb. **63:** 467. 1930; Danser, Blumea **1:** 69. 1934; Merr. & Perry, Jour. Arnold Arb. **23:** 416. 1942.

NOMENCLATURE. Schumann based his description of *Fagraea pachyclados* on a single collection, *Rodatz & Klink 213*, gathered July 4, 1899. The locality given by Schumann is "Kaiser-Wilhelmsland: Bismarck-Gebirge." The holotype is mentioned by Melchior (cited above) as deposited in the Berlin herbarium, and therefore may be presumed destroyed. I have not seen any representatives of the type collection, although from Schumann's protologue there is no question concerning the identity of the taxon which the holotype represented. I therefore designate Schumann's description the lectotype.

A minor nomenclatural matter concerns the gender of the name *Mastixiodendron*. Recommendation 75A of the Code states that Greek generic names ending with "*-dendron*" should be considered neuter, regardless of the gender assigned to them by publishing authors. Consequently, some recent authors have altered the epithet of the type species of *Mastixiodendron* from *pachyclados* (masculine) to *pachycladon* (neuter) in order that it agree grammatically with the generic name. However, such agreement between the name of a genus and an epithet is required only if the epithet is adjectival. Schumann originally employed the epithet *pachyclados* in combination with the feminine generic name *Fagraea*; Melchior used the same epithet with *Mastixiodendron*. Such usage suggests that *pachyclados* ought to be regarded as an appositive noun not necessarily agreeing with the generic name. I have consequently maintained *M. pachyclados* as the name of the type species.

DISTRIBUTION AND ECOLOGY. The typical variety of *Mastixiodendron pachyclados* extends from the northern Moluccas eastward through New Guinea and the Bismarck Archipelago, and in altitude from near sea level to about 1100 meters. Populations frequently occur as pure or nearly pure stands in primary or secondary forests, on level or mountainous terrain, and often on clayey or sandy soils. Flowering and fruiting specimens have been gathered throughout the year.

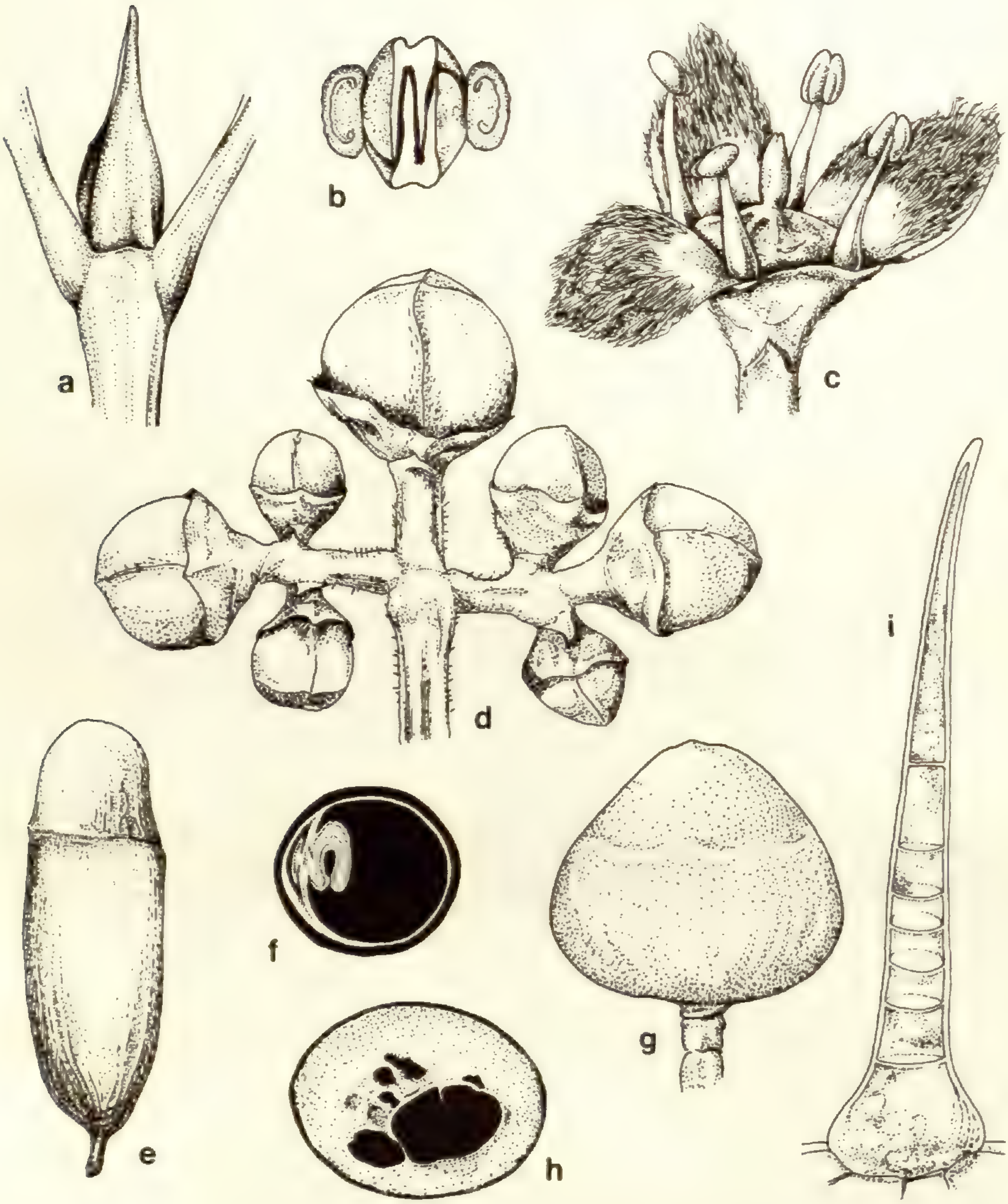


FIGURE 10. a–h, *Mastixiodendron pachyclados* var. *pachyclados*: a, stipule pair in terminal bud, × 1 (from *BW 8130 (Noesi)*); b, terminal bud in cross section showing imbricate stipules flanked by leaf bases, × 2 (from *Hoogland 4925*); c, flower with one corolla lobe removed, × 8 (from *Katik W2880*); d, terminal portion of inflorescence branch showing young and late flower buds, × 8 (from *Katik W2895*); e, fruit, × 2 (from *Hoogland 4925*); f, fruit in cross section showing developed and aborted seeds, × 2 (from *Brass 14097*); g, subglobose fruit, × 2 (from *NGF 36017 (Kumul)*); h, same in cross section, × 2. i, *Mastixiodendron pachyclados* var. *tomentosum*: trichome from abaxial surface of leaf blade showing relatively thick outer wall and thinner partitions, × 2500 (from *BW 1557 (Schram)*).

LOCAL NAMES. "Modjiu," "raimagogo" (Moluccas), "teitakka" (Manikiong), "ngoewaai" (Hattam), "siëk" (Noemfoor), "kriweek" (Biak), "koerdop" (Samber-Japen), "not-notie" (Kwesten), "klaoedi" (Kentoek), "kraoedu" (Kemtoek), "ambehend" (Tami), "loe," "maneu" (Iko), "woent" (Waris), "igo" (Nemo), "wamami" (Timbunke), "monnampun" (Kaigorin), "monnanden" (Rawa), "garo garo" (Dawa Dawa), "aimo" (New Britain).

Moluccas.[1,2] MOROTAI: Tobelo, north Totodokoe, *bb 33742* (*Tangkilisan 31*) (A, BRI, L, LAE); Totodokoe, *bb 33768* (*Tangkilisan 72*) (A, BRI, L, LAE); Tilai River, *bb 33890* (*Tangkilisan 2171*) (L); Sangowo, *Kostermans 1044* (A, L); Sangowo River, *Kostermans 1408* (A, L, NY). TERNATE: Bantjan, *bb 16464* (L). HALMAHERA: Weda, Tiloppe, *bb 24870* (A, L), *bb 24896* (L). CERAM: Kiandarat, *bb 25860* (L); Rioeapa River, *Rutten 1604* (L). **West New Guinea.** VOGELKOP: Manaswari Island, Mansinam, *Herb. Beccari 9984a* (L); Manokwari, Oransbari *BW 1555* (*Schram*) (A, CANB, K, L, LAE), *BW 4570* (*Lasschuit*) (CANB, L, LAE). GEELVINK BAY: Noemfoor Island, Biak, *BW 1019* (*Koster*) (L); Noemfoor Island, *NGF 312* (LAE); Japen Island, Soemberbaba, *BW 11141* (*Koster*) (A, BRI, CANB, K, L, LAE); Japen Island, Aisao, *BW 10558* (*Schram*) (L). DJAJAPURA: Takar, *BW 2279* (*Mangold*) (L, LAE); Sekoli, *BW 8130* (*Noesi*) (CANB, L, LAE); Sekoli-vlakte, *BW 9398* (*Schram*) (CANB, L, LAE); Sekoli, south of Lake Sentani, *BW 9462* (*Schram*) (CANB, L, LAE); Hollandia, *BW 4819* (*Versteegh*)* (CANB, L); Dozai, *Kostermans & Soegong 400* (A, L); Tami, Holtekang, *BW 824* (*Brouwer*) (A, CANB, L, LAE); mouth of Tami River, *BW 2677* (*Schram*) (CANB, L, LAE), *BW 2682* (*Schram*) (CANB, L, LAE); Tami, *BW 1640* (*Schram*) (CANB, L, LAE); Nemo, *BW 2791* (*Schram*) (L), *BW 3473* (*Kalkman*) (A, CANB, K, L, LAE); Idenburg River, Bernhard Camp, *Brass 14097* (A, BM, BRI, L, LAE), *Brass & Versteegh 13548* (A, BM, BRI, K, L). **Northeast New Guinea.** WEST SEPIK: vicinity of Vanimo, Yakara Hill, *NGF 36017* (*Kumul*)* (A, BRI, CANB, L, LAE); Aitape, *NGF 514* (*McAnalan*) (A, BRI, LAE), *NGF 523* (*McAnalan*) (A, BRI, LAE); southeast of Tadji Airstrip, *NGF 1200* (*L. S. Smith*) (A, BRI, CANB, K, L, LAE); Yellow River, near Sepik River, *NGF 3860* (*Womersley*) (L, LAE). EAST SEPIK: north of Timbunke, on track to Kwoiwut, *Pullen 1676** (A, CANB, L, LAE). MADANG: Josephstaal, *NGF 10305* (*K. J. White*) (LAE); Aiome, south side of Asai River, *NGF 27482* (*Henty*) (CANB, L, LAE); Gogol River, *NGF 46521* (*Katik*)* (BRI, L, LAE); Gogol Base, *Oswell W2668* (LAE), *Katik W2737* (L, LAE); south of Gogol River, vicinity of Mawan, *Hoogland 4925* (A, CANB, K, L, LAE); Aupan logging area, *Katik W2880* (A, BISH, CANB, L, LAE), *W2882* (A, BRI, CANB, L, LAE), *W2884* (L, LAE), *W2886* (L, LAE), *W2891* (LAE), *W2892* (LAE), *W2895* (BRI, CANB, K, L, LAE), *W2896* (L, LAE), *W2897* (BRI, L, LAE); Amiaba River, *NGF 45877* (*Foreman et al.*) (A, BISH, CANB, L, LAE). MOROBE: Bulolo felling area, *NGF 10145* (*K. J. White*) (LAE); Ganalangumbum, *NGF 26086* (*Streimann*) (LAE). **Papua.** GULF: Vailala River, above Lohiki, *Pullen 6451* (CANB, LAE); vicinity of Lohiki village, *Schodde 4278* (A, L, LAE); Ihu Hill, northwest of Ihu, *Schodde 4245* (A, CANB, L, LAE); Ihu, *Brass 943* (A); vicinity of Putei, junction of Tauri and Kapau Rivers, *Craven & Schodde 954* (CANB). CENTRAL: Trans Brown, *NGF 17392* (*Havel & Kairo*) (A, BRI, CANB, L, LAE, US);

[1] Abbreviations of institutional collecting series and the names of geographical subdivisions in New Guinea and the Bismarck Archipelago follow Coode, 1973.

[2] Collections of *M. pachyclados* var. *pachyclados* marked with an asterisk (*) have subglobose fruits.

Cape Rodney, *Dobson 1393* (K, LAE), *NGF 38581 (Henty)* (A, BISH, BRI, CANB, K, L, LAE). NORTHERN: vicinity of Siurane, south side of Hydrographers Range, *Pullen 5534* (CANB). MILNE BAY: river bank and flats about 1.6 km. up Dawa River, *NGF 1334 (L. S. Smith)* (A, L, LAE); Milne Bay, without further locality. *McAdam s.n.* (LAE). **Bismarck Archipelago.** NEW BRITAIN: vicinity of Urin, South New Britain, *NGF 10036 (K. J. White)* (A, L, LAE). NEW IRELAND: inland from Lavongai, *NGF 29673 (Coode & Cropley)** (A, BISH, BRI, CANB, L, LAE); New Hanover, Taskul, *Coode 3734* (LAE). MANUS: Kaguli Ridge, *LAE 59236 (Foreman & Katik)** (BISH, LAE).

1b. **Mastixiodendron pachyclados** var. **tomentosum** S. Darwin, var. nov.

FIGURE 10, i.

Arbor idem ac varietas typica sed foliorum laminis subtus in nervis et laminis pilis dispersis effusis stramineis vel fuscis ad 0.5 mm. longis pilosis vel puberulis differt.

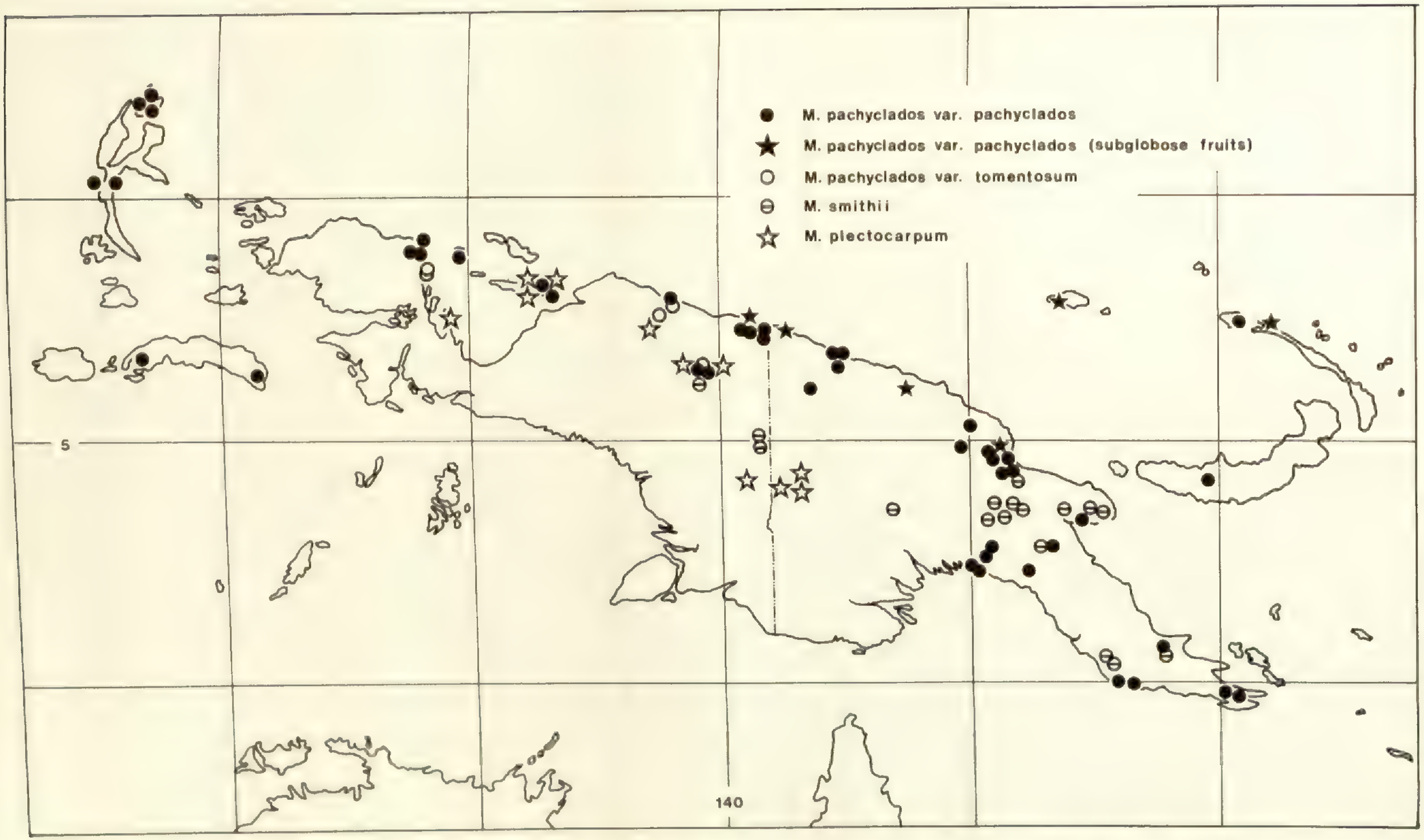
NOMENCLATURE. The type of this new variety is *BW 4569* (cited below) collected by J. A. Lasschuit on February 1, 1958, at Oransbari, Vogelkop, West New Guinea, in an area of primary forest, sandy soil, and at about 15 meters altitude. Specimens were gathered from a tree 40 meters high with a trunk about 98 cm. d.b.h. The flowers are noted as being green when alive. Mature fruits have not been seen.

DISTRIBUTION AND ECOLOGY. Thus far known only from West New Guinea, *Mastixiodendron pachyclados* var. *tomentosum* is frequently encountered on the east coast of the Vogelkop Peninsula. Other collections have been made in coastal areas of Djajapura and farther inland near the Idenburg River. This variety is commonly a tree of the primary forest, growing on rocky, sandy, clayey, or limestone soils and at altitudes from near sea level to about 50 meters. Flowering specimens have been gathered in February and November; a specimen with very young fruits, in October.

LOCAL NAMES. "Teitakka," "tladdjni" (Manikiong), "benggvewai" (Waean), "nggoeway" or "ng-goewaai" (Hattam), "bakwiet" (Kwesten), "elieuw" (Berik).

West New Guinea. VOGELKOP: vicinity of Andai, southwest of Manokwari, *BW 11825 (Koster)* (L, LAE); Oransbari, *BW 1128 (Koster)* (CANB, L, LAE), *BW 1557 (Schram)* (CANB, L, LAE), *BW 1929 (Schram)* (A, CANB, K, L, LAE), *BW 1949 (Schram)* (L), *BW 2125 (Mangold)* (CANB, L, LAE), *BW 2527 (Brouwer)* (L), *BW 4542 (Lasschuit)* (L), *BW 4569 (Lasschuit)* (CANB, holotype; isotypes at A, L, LAE), *BW 4571 (Lasschuit)* (L), *BW 4577 (Lasschuit)* (CANB, L, LAE), *BW 7301 (Hildebrand)* (LAE). DJAJAPURA: Takar, *BW 2270 (Mangold)* (CANB, L, LAE); near bivouac Oereb, *BW 9068 (Iwanggin)* (CANB, L, LAE); Bernhard-bivak, *bb 25675* (L).

Mastixiodendron pachyclados is by far the most frequently collected species of that genus in Papuasia (the only species which extends into the Moluccas), and is readily distinguished by its robust branchlets, leaves,



MAP 1. Collection sites of some species of *Mastixiodendron* in the Moluccas, New Guinea, and the Bismarck Archipelago.

and inflorescences. The leaves especially are distinct in their large size, frequently rounded apices, and stout petioles. Leaves with bluntly cuspidate apices are common in collections from the Moluccas (in which instances the leaves are also often very large), but cuspidate, obtuse, and rounded apices may occur in single specimens from New Guinea. In a few collections (*e.g.*, *NGF 17392* (*Havel & Kairo*) and *NGF 1334* (*L. S. Smith*), from southeastern Papua) the leaves may be consistently obtuse and closely resemble those of *M. smithii*, although the branchlets have a robustness more characteristic of the present species.

The inflorescences of *Mastixiodendron pachyclados* usually have stout peduncles and pedicels and are about as broad as long, frequently with more than 500 flowers. Inflorescences of other species are usually not so large and are longer than broad. The flowers of the present species are recognized by their comparatively short and spreading calyx limbs, by the particularly fleshy corolla lobes, and by the flower buds which are four-angled and about as broad as long. Flowers and flower buds of similar proportion are found in *M. robustum*, from Fiji, but that species differs strongly in its smaller, fewer-flowered inflorescences and smaller leaves, among other characters. The flowers of *M. smithii* differ in their corolla lobes, which are densely puberulent outside, and in the disc, which is subconical and puberulent.

The fruits of *Mastixiodendron pachyclados* are usually long-ellipsoid or subcylindrical. They are aromatic, but lack strongly cancellate tissue. As indicated by the position of the perianth scar, the ovary is seldom more than half superior. The fruits are nearly globose when young but gradually elongate, although in a few collections the fruits remain subglobose or turbinate at maturity; in at least one collection (*Coode 3734*, from New Hanover), the fruits are somewhat intermediate between globose and cylindrical, and have relatively thick walls. The occurrence of subglobose fruits is occasionally associated with relatively large flowers (e.g., *NGF 29673* (*Coode & Cropley*)), but is not reliably correlated with any other floral or vegetative characters. In addition, the subglobose fruits which I have examined are sterile, possibly as the result of insect damage. I therefore have not given collections with subglobose fruits any formal taxonomic recognition, even though they are geographically restricted to the Bismarck Archipelago and the north coast of New Guinea (MAP 1). Until such time as they can be studied in greater detail, I retain those collections within the typical variety of the present species.

Specimens of *Mastixiodendron pachyclados* are usually glabrous except for the inflorescences, which are finely puberulent. However, in a few collections the lower surfaces of the leaf blades are puberulent to pilose. Similar variability in indumentum is evident among Fijian species of *Mastixiodendron*, but in those instances the presence or absence of indumentum on the leaf blades correlates well with numerous other features of the inflorescences, flowers, and fruits. Most available collections of *M. pachyclados* with pubescent leaf blades are sterile, but in the few cases where flowering inflorescences are present they are similar to those of

glabrous specimens. The pubescence on the leaf blades of a few collections might therefore be attributed to random variation were it not that such collections show a reasonably discrete geographical distribution (MAP 1). For that reason I recognize them as comprising a new variety, *M. pachyclados* var. *tomentosum*.

2. **Mastixiodendron smithii** Merr. & Perry, Jour. Arnold Arb. **26**: 255. 1945. FIGURES 1; 8; 11, a–d.

Tree to 45 m. high, the bole often twisted, to 27 m. high, to 3 m. d.b.h., the buttresses few, to 4 m. high, the crown narrow and compact; bark variable from pale green-brown to black, smooth to fissured, often pustular to flaking, the inner bark and wood white to pale yellow-brown, darkening on exposure; branchlets 3–5(–7) mm. broad toward apex, dark red-brown, becoming pale gray to brown; mature stipules lanceolate to oblong-lanceolate, 25–35 mm. long, 8–10 mm. broad, long acuminate at apex; petioles relatively stout, semiterete, 15–25(–35) mm. long, 2.5–4 mm. broad, winged by base of leaf blade; leaf blades coriaceous, elliptic to obovate, (8–)10–21 cm. long, (4–)5–10 cm. broad, acute to obtuse and bluntly cuspidate at apex, often somewhat revolute at margin, glabrous and glossy above, glabrous and often paler beneath, the costa conspicuous, plane to prominulous above, raised and rounded beneath, the secondary nerves 9 to 13 per side, prominulous above, more prominent beneath, the tertiary nerves and veinlets prominulous above and beneath; inflorescences finely puberulent with minute, scattered, stramineous hairs to 0.1 mm. long, relatively robust, open, with 2 to 3 orders of branching and as many as 450 flowers, 9–12 × 6–15 cm. at anthesis, considerably larger in fruit, the peduncles subterete, 1–5 cm. long, 2–4 mm. in diameter, the inflorescence bracts deltoid, to 1 mm. long, to 0.5 mm. broad at base, acute to acuminate at apex; pedicels slender, 3–4 mm. long; calyx limb cupular, 2–3 mm. across, the lobes coriaceous to membranaceous, deltoid to broadly ovate, 0.5–1(–1.5) mm. long, about 1 mm. broad, acute to nearly cuspidate at apex, united at base into shallow cup to 0.5 mm. high, glabrous to minutely puberulent outside with scattered hairs; corolla limb to 9 mm. across, the lobes green to white, lanceolate to ovate to oblong, 3.5–4.5 mm. long, 1.2–1.6 mm. broad, minutely but densely puberulent outside with gray to stramineous hairs, densely pilose over most of surface inside with lax, tangled, stramineous to yellow hairs to 1.2 mm. long, glabrous toward base; filaments of stamens 2.5–3.5 mm. long, about 0.3 mm. broad at base, tapering toward apex, the anthers 0.5–0.8 mm. long, about 0.5 mm. broad; inferior portion of ovary 1.5–2 × 1.5(–2.5) mm., the disc subconical, about 1 mm. high, to 1.5 mm. broad at base, blunt at apex, minutely but densely puberulent to papillate with gray to stramineous hairs less than 0.05 mm. long; style about 2 mm. long, about 0.2 mm. in diameter, truncate or divided about 0.2 mm. at apex; fruits hard, fibrous to woody, pale yellow-green to gray-green, glabrous, ovoid to broadly fusiform, often subquadrangular, 48–70 × 20–30 mm., ringed by perianth scar less than

FIGURE 11. a–d, *Mastixiodendron smithii*: a, flower with one corolla lobe removed, × 10 (from *NGF 29193* (*Henty & Coode*)); b, terminal and one lateral branch of dichasium showing flower buds, × 8 (from *NGF 29193* (*Henty & Coode*)); c, fruit, × 1 (from *NGF 1022* (*L. S. Smith*)); d, fruit in cross section showing two locules and areas of cancellate tissue, × 1 (from *Carr 14789*). e–h, *Mastixiodendron stoddardii*: e, flower with one corolla lobe removed, × 5

10 mm. below usually pointed apex, the mesocarp fleshy, to 1 mm. thick, the endocarp cancellate with cavities filled with yellow to reddish resin; seeds to 22 × 4 mm., yellow-brown, often folded lengthwise when dry.

NOMENCLATURE. The type of *Mastixiodendron smithii* is *Clemens 5154*, cited below. The locality given on the holotype is "Ogeramnang" (Ogeranang in eastern Morobe district). The type collection, in late flowering condition, was gathered at an altitude of about 1800 meters from a tall tree growing on a forested hillside. The flowers were whitish green. An herbarium stamp suggests that an isotype may have been deposited at Berlin.

DISTRIBUTION AND ECOLOGY. The present species is endemic to New Guinea, occurring principally in the eastern portions of Northeast New Guinea and Papua, but with populations extending into central West New Guinea. Isolated individuals of *Mastixiodendron smithii* have been collected at altitudes from 800 to 1900 meters in primary or secondary forests. Flowering and fruiting specimens have been gathered throughout the year.

LOCAL NAMES. "Umani" (Eastern Highlands), "nowaki" (Aiyura), "pein" (Akuna), "china" (Anona), "tsekigi" (Kutubu), "naháterеh" (N. Managalase).

West New Guinea. DJAJAPURA: Idenburg River, 6 km. southwest of Bernhard Camp, *Brass & Versteegh 12517* (A, L). SNOW MOUNTAINS: headwaters of Ok Denim River, *NGF 33079 (Henty et al.)* (A, CANB, K, L, LAE), *NGF 33211 (Henty et al.)* (A, BRI, CANB, L, LAE). **Northeast New Guinea.** MADANG: Budemu, *NGF 21328 (Sayers)* (A, BM, L). MOROBE: Araulu logging area, *LAE 62089 (Katik & Eddowes)* (BISH, LAE, US); Boana, *Clemens 5154* (A, holotype; L, isotype); Yunzaing, *Clemens 3723* (A, L). EASTERN HIGHLANDS: Kassam Pass, *NGF 29193 (Henty & Coode)* (A, CANB, L, LAE), *NGF 29351 (Henty & Vandenberg)* (A, CANB, L, LAE); Aiyura, *NGF 1022 (L. S. Smith)* (A, BRI, LAE), *NGF 3381 (Womersley)* (A, CANB, K, L, LAE); vicinity of Okapa, *Hornibrook 182A* (LAE); vicinity of Perosa, about 29 km. southwest of Okapa, *Hartley 13182* (A, CANB, L, LAE). **Papua.** SOUTHERN HIGHLANDS: vicinity of Moro, Lake Kutubu, *Schodde 2402* (CANB, L, LAE). CENTRAL: Boridi, *Carr 13272* (BM, L), *14788* (BM, L), *14789* (A), LAE *60289 (Foreman & Vinas)* (A, BISH, LAE). NORTHERN: south side of Hydrographers Range, vicinity of Siurane, *Pullen 5472* (CANB, L, LAE).

Mastixiodendron smithii is a very distinct species, easily recognized by its more or less oblong flower buds and minute but dense puberulence on the outside of the corolla lobes. As the fruit matures and the corolla falls away, a similar indumentum becomes obvious on the subconical disc. The fruits are also remarkable for their comparatively large size, the perianth scar, which is located near the usually sharply pointed apex, and the woody to fibrous interior with resin cavities.

(from *BSIP 10145 (Sirute'e et al.)*); f, terminal flower of dichasium in bud. × 8 (from *BSIP 10159 (Gafui et al.)*); g, fruit, × 2 (from *BSIP 9118 (Gafui et al.)*); h, same in cross section showing developed and aborted seeds, × 3.

In all of the above features, the present species is distinct from *Mastixiodendron pachyclados*, which also differs in its larger inflorescences, often rounded leaf apices, and stouter branchlets, among other characters. Merrill and Perry (cited above) compared *M. smithii* with *M. stoddardii*, which is similar in the shape and size of its leaves. However, in the latter species the corolla lobe exteriors and the more rounded discs are glabrous, and the flower buds are ovoid rather than oblong. The fruits of *M. stoddardii* are frequently more than half superior and are comparatively thin-walled.

The closest ally of *Mastixiodendron smithii* is probably *M. plectocarpum*. In both taxa the flower buds and the expanded corolla lobes are similarly shaped, and the corolla lobe exteriors in the latter species may be somewhat puberulent; the disc in *M. plectocarpum* is likewise puberulent, although it is flat rather than subconical. As to fruits, there can be little confusion between those of the present species and those of *M. plectocarpum*, which, although strongly cancellate, are much smaller and rounded at the apex. The two species further differ in vegetative characters, *M. plectocarpum* generally having more delicate branchlets, petioles, and inflorescences, as well as smaller and usually narrower leaf blades with finer venation. In one collection (*Brass & Versteegh 12517*, from West New Guinea), I have found fruits of the *M. plectocarpum* type associated with vegetative parts and young flower buds clearly referable to *M. smithii*. However, because the fruits are not attached, and since the collectors gathered specimens of both species at the same locality, it is possible that the collection represents an unintentional admixture and not a morphologically "intermediate" entity.

3. **Mastixiodendron stoddardii** Merr. & Perry, Jour. Arnold Arb. **26**: 254. 1945; Whitmore, Guide Forests Brit. Solomon Isl. 95. 1966.

FIGURES 4; 11, e–h.

Mastixiodendron Smithii sensu Walker, Forests Brit. Solomon Isl. Prot. 162. 1948; non Merr. & Perry.

Tree to 30 m. high, the bole often poorly formed, about 1 m. d.b.h., the buttresses thick, to 3 m. high, the crown small, dense, with heavy, ascending limbs; bark pale to dark gray or brown, narrowly fissured, papery and flaking, the inner bark and wood white to pale yellow-brown, darkening on exposure, and with the odor of linseed oil; branchlets 2–4 mm. broad toward apex, dark red-brown, becoming pale gray-brown; mature stipules elliptic to lanceolate, 13–22 mm. long, to 8 mm. broad, acuminate at apex; petioles relatively slender, semiterete to somewhat canaliculate, 10–25(–30) mm. long, to 2.5 mm. broad, winged by base of leaf blade; leaf blades coriaceous to chartaceous, elliptic to occasionally obovate, 7–23 cm. long, 3–11 cm. broad, acute or acuminate or bluntly cuspidate at apex, glabrous, often drying paler beneath, the costa conspicuous, plane to somewhat canaliculate above, raised and rounded beneath, the secondary nerves 10 to 16 per side, prominulous above, raised and rounded

to prominulous beneath, the tertiary nerves and veinlets prominulous to plane above and beneath; inflorescences finely puberulent with scattered, minute hairs, relatively delicate, open, often more or less flat-topped, usually with 2 orders of branching and 15 to 40 flowers, 7–8.5(–12) × 3.5–7(–9) cm. at anthesis, 11–15 × 5–16 cm. in fruit, the peduncles slender, (1–)3.5–6.5(–10) cm. long, 1–1.5 mm. in diameter, the inflorescence bracts subdeltoid, to 1 mm. long, to 1 mm. broad at base, acuminate at apex; pedicels slender, (3–)4–5 mm. long; calyx limb cupular, to 4.5 mm. across, the lobes coriaceous to membranaceous, deltoid, 0.5–1 mm. long, 1–2 mm. broad, acuminate to obtuse and apiculate at apex, united at base into shallow cup to 0.5 mm. high, glabrous outside; corolla limb about 10 mm. across, the lobes pale yellow-green, deltoid to ovate, 3–4 mm. long, 1.5–2.5 mm. broad, essentially glabrous outside, densely pilose distally inside with lax, tangled, yellow hairs to 1.5 mm. long, glabrous toward base; filaments of stamens 2.5–3 mm. long, about 0.3 mm. broad at base, tapering toward apex, the anthers 0.8–1 mm. long, about 0.5 mm. broad; inferior portion of ovary to 1 mm. long, about 2 mm. broad, the disc broadly ovoid, 1.5–2 mm. high, 2–2.5 mm. broad at base, glabrous; style 1–1.5 mm. long, about 0.3 mm. in diameter, truncate to rounded at apex; fruits hard, pale green when alive, drying pale brown to black, glabrous, ovoid or rarely oblong, gradually tapering toward apex, 25–45 mm. long, 8–13 mm. broad, ringed by perianth scar 15–25 mm. below apex, the mesocarp thin and dense, the endocarp hard, bony, 0.5–2 mm. thick; seeds about 24 × 5 mm., yellow- to red-brown.

NOMENCLATURE. The type collection named by Merrill and Perry is *Stoddard 12*. The holotype is a flowering specimen from "Banika Island in Russell Islands," without further locality.

DISTRIBUTION AND ECOLOGY. *Mastixiodendron stoddardii* is known from Guadalcanal, from surrounding islands of the Solomon Islands, and from New Britain in the Bismarck Archipelago. The species occurs in well-drained, forested areas at altitudes of 60 to 350 meters. Flowering and fruiting specimens have been collected throughout the year.

LOCAL NAMES AND USE. The following names, all from the Solomon Islands, have been noted: "kakarafua" or "kakarahua" (Kwara'ae), "aitalinge" or "aisalinga" (Longu), "haipatchou" (Guadalcanal), and "mumu" (Malaita). The present species is said to have a hard, durable wood suitable for construction, although the ill-formed bole would preclude its use in commerce.

Bismarck Archipelago. NEW BRITAIN: west branch of Fullerborn Harbor, *NGF 21741 (Sayers)* (A, CANB, L, LAE); Powell Harbor, *LAE 52106 (Foreman)* (K, LAE). **Solomon Islands.** RUSSELL ISLANDS: Mbanika Island, *Stoddard 12* (A, holotype). GUADALCANAL: Wanderer Bay, ridge west of Mbilikovu River, *BSIP 9110 (Gafui et al.)* (L), *BSIP 9118 (Gafui et al.)* (K, L, LAE); west coast behind Nduindui Village, *BSIP 10145 (Sirute'e et al.)* (K, L, LAE); south coast, Kolotsiri Ridge near Nduindui, *BSIP 10159 (Gafui et al.)* (K, L, LAE); Rere River,

about 4.8 km. inland, *BSIP 2791 (Whitmore)* (K, L, LAE), *BSIP 3804 (Whitmore)* (L, LAE); ridge west of Valasi River, *BSIP 326 (Leggate)* (L, LAE); Kaukau Bay, Singgalia River, *BSIP 250 (F. S. Walker)* (A, BRI, K, L). SAN CRISTOBAL: Wairaha River, 8 km. from coast, *BSIP 4228 (Whitmore)* (L, LAE).

In addition to the type collection from the Solomon Islands, Merrill and Perry (cited above) assigned a few fruiting collections from West New Guinea to *Mastixiodendron stoddardii*, although they pointed out differences in vegetative characters between collections from those two localities. Since that first description, more abundant material from the Solomon Islands has shown that the fruits associated with *M. stoddardii*, sensu typi, are not at all like those of New Guinea collections, which are here referred to *M. plectocarpum*.

The fruits of *Mastixiodendron stoddardii* are more or less half superior, relatively thin-walled, and lack a strongly cancellate tissue; in all such respects they resemble the fruits of *M. pachyclados*. However, the fruits of the present species are usually ovoid, rather than ellipsoid or subcylindrical, and are long-tapering toward the apex. A relationship between *M. stoddardii* and *M. pachyclados* is suggested by collections from New Britain (*NGF 21741 (Sayers)* and *LAE 52106 (Foreman)*), which resemble the former species in their vegetative features, but approach *M. pachyclados* in the shape and size of their fruits.

The similarity of *Mastixiodendron stoddardii* to *M. pachyclados* hardly goes further than the structure of the fruits. The broad corolla limb, elongate corolla lobes, open inflorescences, long and slender pedicels, and the leaf blades with acute to acuminate apices all suggest *M. smithii*. However, although the present species shows affinities with both of the above-mentioned taxa, it is nonetheless unique in many of its characters and is reasonably well isolated geographically.

4. **Mastixiodendron plectocarpum** S. Darwin, sp. nov.

FIGURES 7, 9, 12.

Arbor ad 35 m. alta, trunco ad 25 m. alto ad 60 cm. diametro, anteridibus nullis vel complanatis ad 1.5 m. altis et extrinsecus extensis, cortice cinereo-viridi vel brunneola laevi vel subtiliter fissurata et chartacea, cortice interiore et ligno albo vel flavido brunneo sed post expositionem fuscanti; ramulis gracilibus apicem versus 2–3 mm. latis atro- vel pallido-ferrugineis denique cinereo-fuscis et pallidis; stipulis maturis lanceolatis 12–20 × 4–6 mm. apice acutis vel acuminatis; petiolis gracilibus 15–35 mm. longis 1–2.5 mm. latis semiteretibus vel basi subteretibus et lamina folii basi alatis; foliorum laminis coriaceis lanceolatis vel anguste vel late ellipticis 6–19 cm. longis 1.5–6.5 cm. latis apice obtuse vel raro acutissime acuminatis supra glabris nitidis vel glaucis, subtus glabris, costa conspicua supra plana vel prominula subtus elevata, nervis secundariis utrinsecus 15 ad 20 et utrinque prominulis, nervis tertiariis et rete venularum utrinque prominulis; inflorescentiis sparsim puberulis, subtilibus diffusis ramificationis 2 vel 3 ordinibus et cum usque ad 100 floribus, sub anthesi

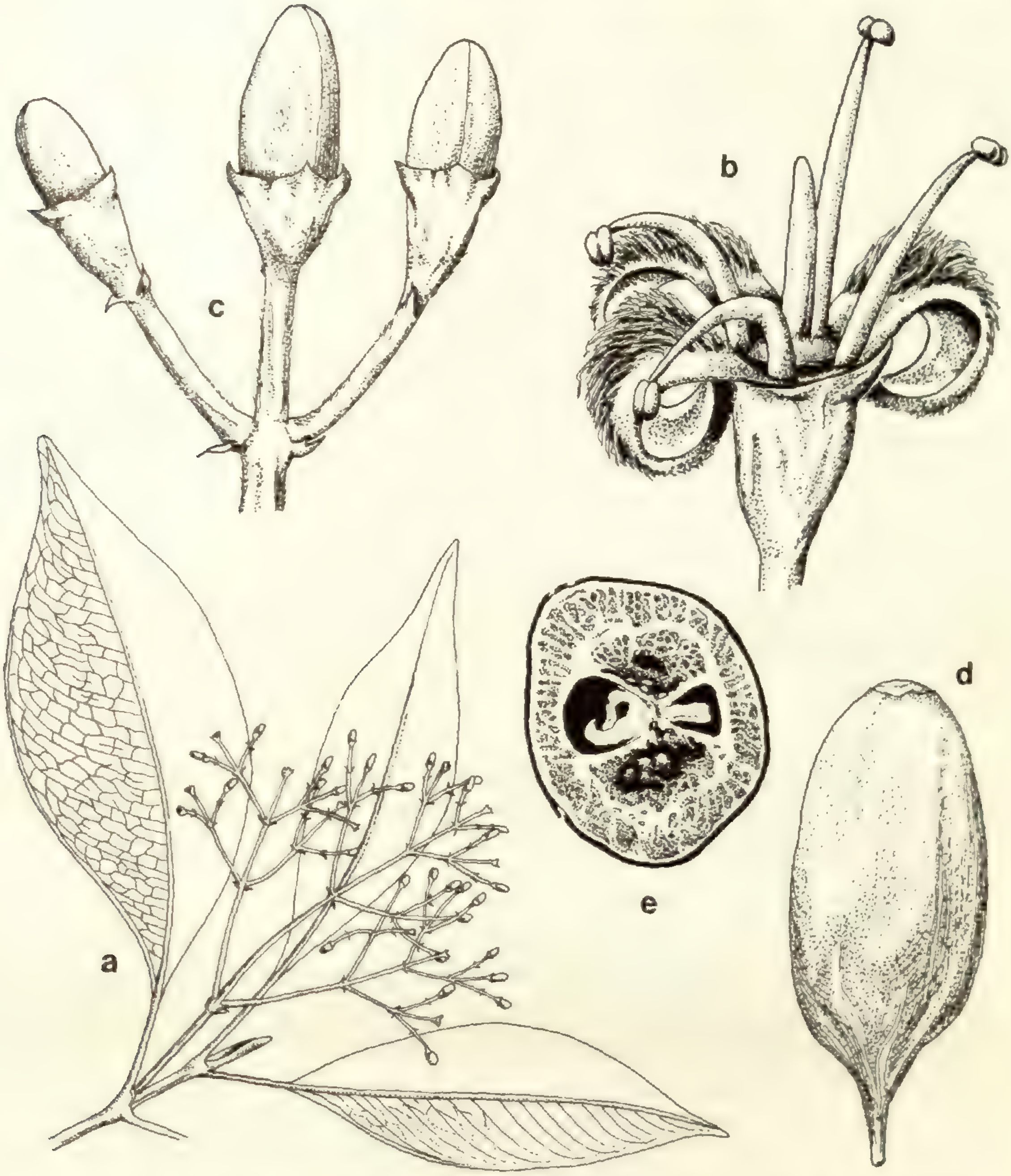


FIGURE 12. *Mastixiodendron plectocarpum*: a, terminal portion of branchlet showing inflorescence shortly before anthesis, × ½ (from *Pullen 7327*); b, flower with one corolla lobe removed, × 10 (from *BW 13347 (Schram)*); c, dichasium with flower buds, × 8 (from *BW 8516 (Kalkman)*); d, fruit, × 2 (from *Kiunga ref. 3*); e, fruit in cross section, × 2 (from *Brass & Versteegh 13563*).

(6–)9–11 × (3–)4–12 cm. sub fructu 7–14 × 4–16 cm., pedunculis gracilibus subteretibus 1.5–4(–5) cm. longis et 1–2 mm. diametro, inflorescentiarum bracteis deltoideis vel ovatis ad 1.5 × 1.5 mm. basi saepe amplectentibus apice obtusis vel acuminatis; pedicellis gracilibus ad 5 mm. longis; calycis limbo 1.5–2 mm. lato, lobis submembranaceis late deltoideis vel ovatis ad 0.8 mm. longis 1–1.5 mm. latis basi aliquantum connatis apice acutis vel obtusis et apiculatis extus glabris vel minute puberulis; corollae limbo 5–8 mm. lato, lobis ellipticis vel oblongis vel ovatis 3–4 mm. longis circiter 1 mm. latis flavo-virentibus extus pilis dispersis stramineisque mi-

nute puberulis vel glabris intus distaliter pilis implexis ad 0.8 mm. longis albis vel stramineis pilosis sed basi glabris; staminum filamentis ad 3.5 mm. longis basi circiter 0.2 mm. latis apicem versus angustatis, antheris 0.3–0.5 mm. longis circiter 0.3 mm. latis; ovarii parte inferiore 1–1.5 × 1–1.5 mm., disco applanato ad 0.5 mm. alto in centro depresso et pilis minutis flavis vel albis circiter 0.1 mm. longis puberulo sed marginem versus glabro; stylo 1.5–2 mm. longo circiter 0.2 mm. diametro apice truncato vel ad 0.3 mm. diviso; fructibus ovoideis vel obovoideis (20–)25–30 mm. longis 10–16 mm. diametro basim versus saepe angustatis apice late rotundatis et perianthii cicatrice coronatis, in vivo pallide viridibus in sicco cinereo-purpureis vel nigris, mesocarpio tenui, endocarpio fibroso cancellato et resina aromatica rubella vel pellucida copiose pleno; seminibus 10–12 × 2–3 mm. pallide ferrugineis glabris et in sicco saepe rugosis et longistrorsum plicatis.

NOMENCLATURE. The type collection of *Mastixiodendron plectocarpum* is *Pullen 7327*; the locality is "near old Niogomban Village, c. 4 mi. S. of D'Albertis Junction, upper Fly River, Western Distr., Terr. of Papua." Specimens with fruits and flowers were gathered from a tree 33.5 meters high growing at an altitude of about 30 meters on low, hilly, forested terrain.

The epithet *plectocarpum* refers to the woven (i.e., strongly cancellate) pericarp by which the fruits of this species are readily distinguished.

DISTRIBUTION AND ECOLOGY. *Mastixiodendron plectocarpum* is distributed from the Geelvink Bay area of West New Guinea (including Japen Island) southeastward to western Papua; its altitudinal range is from 30 to 800 meters. Individuals may be common or occasional in humid lowland to hilly, primary or secondary forests, frequently on sandy or clayey soil. Flowers and fruits have been collected between the months of March and September.

LOCAL NAMES. "Moapi" (Samber), "teitakka" (Manikiong).

West New Guinea. GEELVINK BAY: Japen Island, Seroei, *bb 30311* (L), *bb 30318* (L), *bb 30342* (L), *bb 30355* (A, L), *bb 30463* (L); Japen Island, Biak, Semèni near Seroei, *Aet & Idjan* (*exped. L. J. van Dijk*) *318* (K, L); Japen Island, Aisaoe, *BW 10580* (*Schram*) (L); Wondiwoi Mountains, Wandammen Peninsula, *BW 13347* (*Schram*) (LAE). DJAJAPURA: Sidoarsi Mountains, about 200 km. west of Hollandia, *BW 7987* (*Schram*) (CANB, L, LAE); Idenburg River, Bernhard Camp, *Brass & Versteegh 13563* (A, L); 2 km. southwest of Bernhard Camp, *Brass & Versteegh 13502* (A, BM, L). DIGUL: Omkoeboen, about 60 km. north of Mindiptana, *BW 8516* (*Kalkman*) (CANB, L, LAE). **Papua.** WESTERN: upper Fly River, vicinity of old Niogomban Village, about 6.4 km. south of D'Albertis Junction, *Pullen 7327* (CANB, holotype; isotypes at A, L, LAE); road to Rumginae, 4.8 km. north of Kiunga, *NGF 48441* (*Foreman & Katik*) (A, BISH, CANB, LAE); Kiunga, *For. Prod. Moresby* (*Eddowes & Kumul*) *Kiunga ref. 3* (LAE), *NGF 33429* (*Ridsdale & Galore*) (A, BISH, BRI, CANB, K, L, LAE).

Specimens of *Mastixiodendron* from West New Guinea that have fruits with strongly cancellate pericarps and broadly rounded apices were pro-

visionally referred to *M. stoddardii* by Merrill and Perry (1945). Now that many more collections, both fruiting and flowering, are available from that area, it is evident that they have little to do with *M. stoddardii* but represent a separate species, named here *M. plectocarpum*.

Mastixiodendron plectocarpum comprises individuals with delicate, open, relatively few-flowered inflorescences, flowers with more or less oblong buds and flat, puberulent to papillate discs. The fruits are comparatively small, almost entirely inferior, rounded at the apex, and have fibrous pericarps composed largely of resin cavities. The fruits, discs, and flower buds suggest *M. smithii*, to which the present species is probably related. However, in nearly all other characters *M. plectocarpum* remains distinct. It is easily recognized in the vegetative state by its slender branchlets and frequently narrow leaf blades (especially in collections from Japen Island) with the secondary and tertiary nerves hardly distinguishable from one another and prominulous on both surfaces. Leaf blades of similar aspect are found in *M. robustum*, from Fiji, but the reproductive structures of that species are so entirely different as to preclude any close relationship with *M. plectocarpum*.

5. **Mastixiodendron robustum** A. C. Sm., Pacif. Sci. 23: 390. 1969; J. W. Parham, Pl. Fiji Isl. ed. 2. 278. 1972. FIGURES 3, 13.

Tree to 25 m. high, the bole to 16 m. high, to 80 cm. d.b.h., the buttresses spreading, the crown spreading to dense and round; bark smooth, brittle, finely fissured, the inner bark yellow, darkening on exposure, the wood white; branchlets 3–5 mm. broad toward apex, dark red-brown, becoming pale brown; mature stipules oblong-lanceolate, 15–30 × 6–10 mm., acute at apex; petioles stout, semiterete to somewhat canaliculate, (12–)18–30(–40) mm. long, 2–3 mm. broad, broadly winged by base of leaf blade; leaf blades thickly coriaceous, oblong-elliptic to obovate, (7–)9–17 cm. long, (2.5–)3.5–8 cm. broad, acute to bluntly acuminate at apex, often somewhat revolute at margin, glabrous and often somewhat glossy above, glabrous beneath, the costa conspicuous, prominulous to canaliculate above, prominulous to raised and rounded beneath, the secondary nerves 12 to 20 per side, prominulous above and beneath, the tertiary nerves and veinlets prominulous above and beneath; inflorescences puberulent with minute, scattered hairs, robust, with 1 to 2 orders of branching and 7 to 50 flowers, 2–7 × 2–3.5 cm. at anthesis, to 7 × 9 cm. in fruit, the peduncles stout, subterete, to 2 cm. long, 3–4 mm. in diameter, the inflorescence bracts caducous, subdeltoid, to 1 × 1 mm., acute to obtuse at apex; pedicels stout, 1–3 mm. long (to 4 mm. in fruit); calyx limb patelliform, (2–)3–4 mm. across, the lobes membranaceous, broadly ovate to 0.5 mm. long, to 2 mm. broad, obtuse to apiculate to rounded at apex, united at base into cup to 0.3 mm. high, essentially glabrous outside; corolla limb about 8 mm. across, the lobes yellow to white, ovate to subdeltoid, 2.5–3.5 mm. long, (1.5–)2.5–3.5 mm. broad, glabrous to puberulent outside with a few scattered hairs, densely puberulent distally inside with tangled, yellow

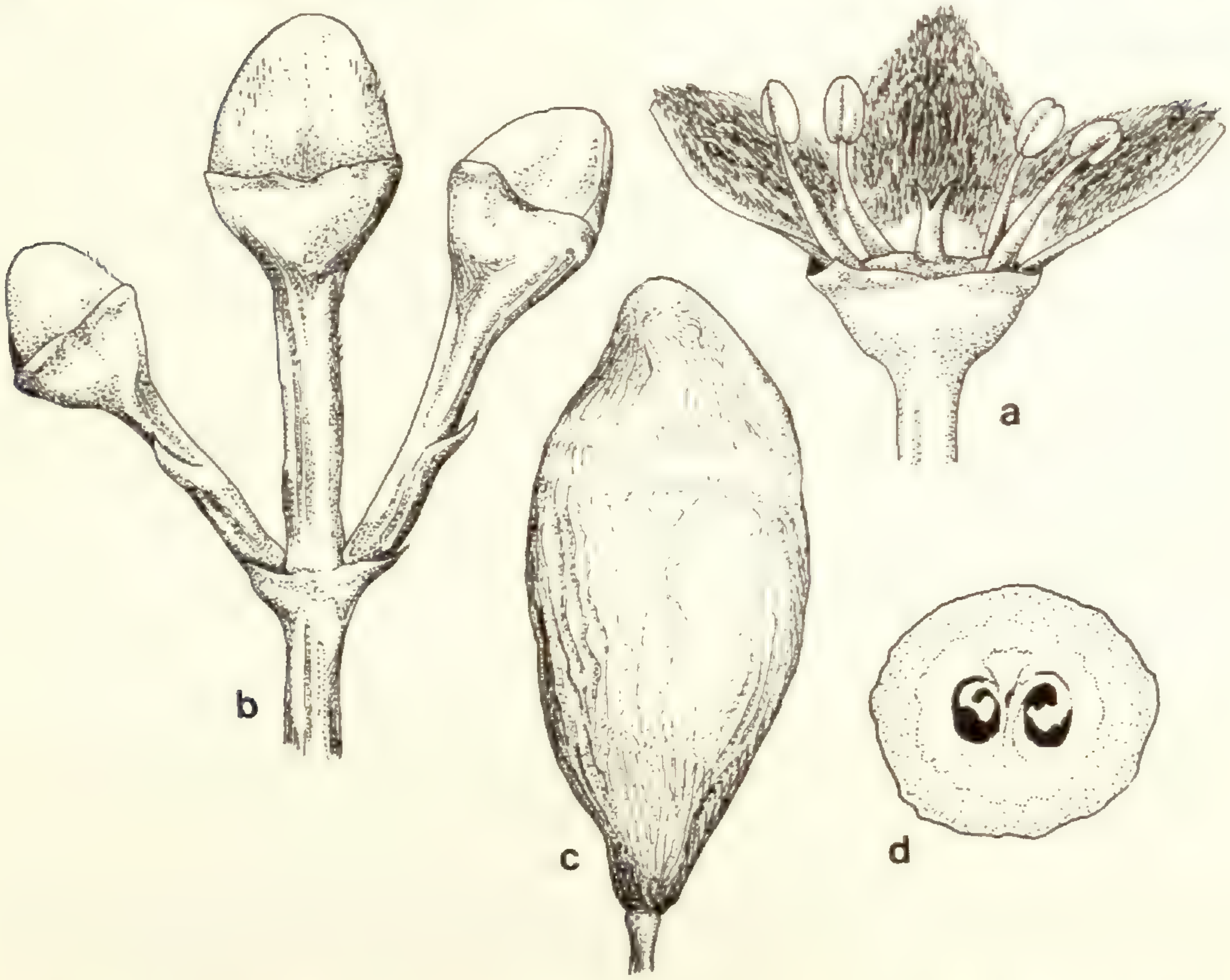


FIGURE 13. *Mastixiodendron robustum*: a, flower with one corolla lobe removed, × 6 (from *Fiji Dept. Agr. L13374*); b, dichasium with flower buds, × 8 (from *Fiji Dept. Agr. L13374*); c, fruit, × 1 (from *W. J. Howard 94*); d, same in cross section, × 1.

hairs to 0.5 mm. long, glabrous toward base; filaments of stamens 1.5–2 mm. long, to 0.5 mm. broad at base, tapering toward apex, the anthers about 0.8 × 0.5 mm.; inferior portion of ovary 1–1.5 mm. long, about 3.5 mm. in diameter, the disc flat to broadly rounded, about 0.5 mm. high, glabrous; style 0.5–1.2 mm. long, about 0.3 mm. in diameter, divided about 0.5 mm. at apex; fruits hard, green to yellowish when alive, drying pale to dark brown, glabrous, ellipsoid to obovoid, (30–)42–55 × (16–)20–26 mm., often tapering toward base, ringed by faint perianth scar 15–20 mm. below rounded to bluntly pointed apex, the mesocarp thin, the endocarp dense, woody, usually without conspicuous resin cavities; seeds 20–35 mm. long, about 3 mm. broad, yellowish brown or orange, wrinkled when dry.

NOMENCLATURE. The type of *Mastixiodendron robustum* is *Fiji Dept. Agr. L13374*, collected near the Waimanu River above Vatuvula, Naitasiri, Viti Levu, at an altitude of 120 meters.

DISTRIBUTION AND ECOLOGY. Endemic to Fiji and known only from the islands of Viti Levu and Vanua Levu. *Mastixiodendron robustum* occurs as a main story tree in forests from near sea level to about 120 meters.

LOCAL NAMES AND USE. I have found the following Fijian names re-

corded: "kauloa" (Viti Levu), "nduvula" (Viti Levu and Vanua Levu). The species is said to yield good, durable timber.

Fiji. VITI LEVU. NAMOSI: Nambukavesi, *Fiji Dept. Agr. 767* (BRI, MASS, SUVA). NAITASIRI: Waimanu River above Vatuvula Village, *Fiji Dept. Agr. L13374* (*Berry 31*, coll. *I. Qoro*) (BISH, holotype; isotypes at K, SUVA). TAILEVU: ridge west of Waisei Village, *Berry 166* (BISH, K, SUVA); Raralevu, *Fiji Dept. Agr. 2667* (BISH, SUVA). REWA: base of Mt. Korombamba, *Fiji Dept. Agr. 1189* (BISH, SUVA). VANUA LEVU. MATHUATA: forests of Mt. Ratinitini, slopes at Seanggangga, *Fiji Dept. Agr. 486* (*Loweth 2256*) (K, SUVA); inland from Lambasa, *Fiji Dept. Agr. 238* (*I. Bola 86*) (BISH, SUVA). THAKAUNDROVE: Navonu Creek, Natewa Peninsula, *W. J. Howard 94* (BISH, K, SUVA). FIJI, without further locality, *E. Damanu NI–32* (K).

This distinct Fijian species has been well discussed by Smith (cited above), and thus its diagnostic characters need only be outlined here. *Mastixiodendron robustum* is readily distinguished by its thickly coriaceous leaf blades with relatively numerous, prominulous secondary nerves. In addition, the branchlets and the reproductive parts are generally more robust than are those of the other Fijian species, as suggested in the key.

Certain specimens of *Mastixiodendron flavidum* approach *M. robustum* in vegetative characters but have the open, freely branched inflorescences and smaller flowers characteristic of the former species. Although the leaf blades of *M. pilosum* are as large as or larger than those of the present species, they are much thinner in texture and pubescent on their lower surfaces; besides many differences in the morphology of their flowers, *M. pilosum* and *M. flavidum* further disagree with the present species in their differently shaped and thinner-walled fruits.

6. Mastixiodendron flavidum (Seem.) A. C. Sm., Jour. Arnold Arb. **26**: 109. 1945; J. W. Parham, Pl. Fiji Isl. 197. 1964, ed. 2. 277. 1972. FIGURES **2**; **14, a–e.**

Rubiacearum gen. (*nov. ?*) Seem., Bonplandia **9**: 257. 1861.
Canthium aff. *lucidum* sensu A. Gray, Proc. Am. Acad. Arts Sci. **5**: 319. 1862. Bonplandia **10**: 36. 1862; non Hooker & Arn.
Canthium flavidum Seem., Fl. Vit. 132. 1866.
Plectronia flavida Bentham & Hooker f. ex Drake, Fl. Ins. Mar. Pac. 194. 1890.
Dorisia rarissima Gillespie, Hooker's Icon. Pl. **32**: *t. 3190*. 1933.
Dorisia flavida A. C. Sm., Bishop Mus. Bull. **141**: 140. 1936; Fosberg, Sargentia **1**: 120. 1942.

Spreading to slender tree or shrub to 20 m. high; branchlets 1.5–3 mm. broad toward apex, dark red-brown, becoming pale brown; mature stipules lanceolate to ovate, 8–22 × 6–8 mm., acuminate at apex; petioles semiterete to somewhat canaliculate, 7–28(–50) mm. long, 1–1.8(–3) mm. broad, winged by base of leaf blade; leaf blades coriaceous, elliptic to oblong-elliptic to obovate, 4–17(–21) cm. long, (1.5–)2–8(–12) cm. broad, obtuse to bluntly acuminate at apex, often somewhat revolute at margin, glabrous and glossy to glaucous above, glabrous or rarely finely puberulent beneath

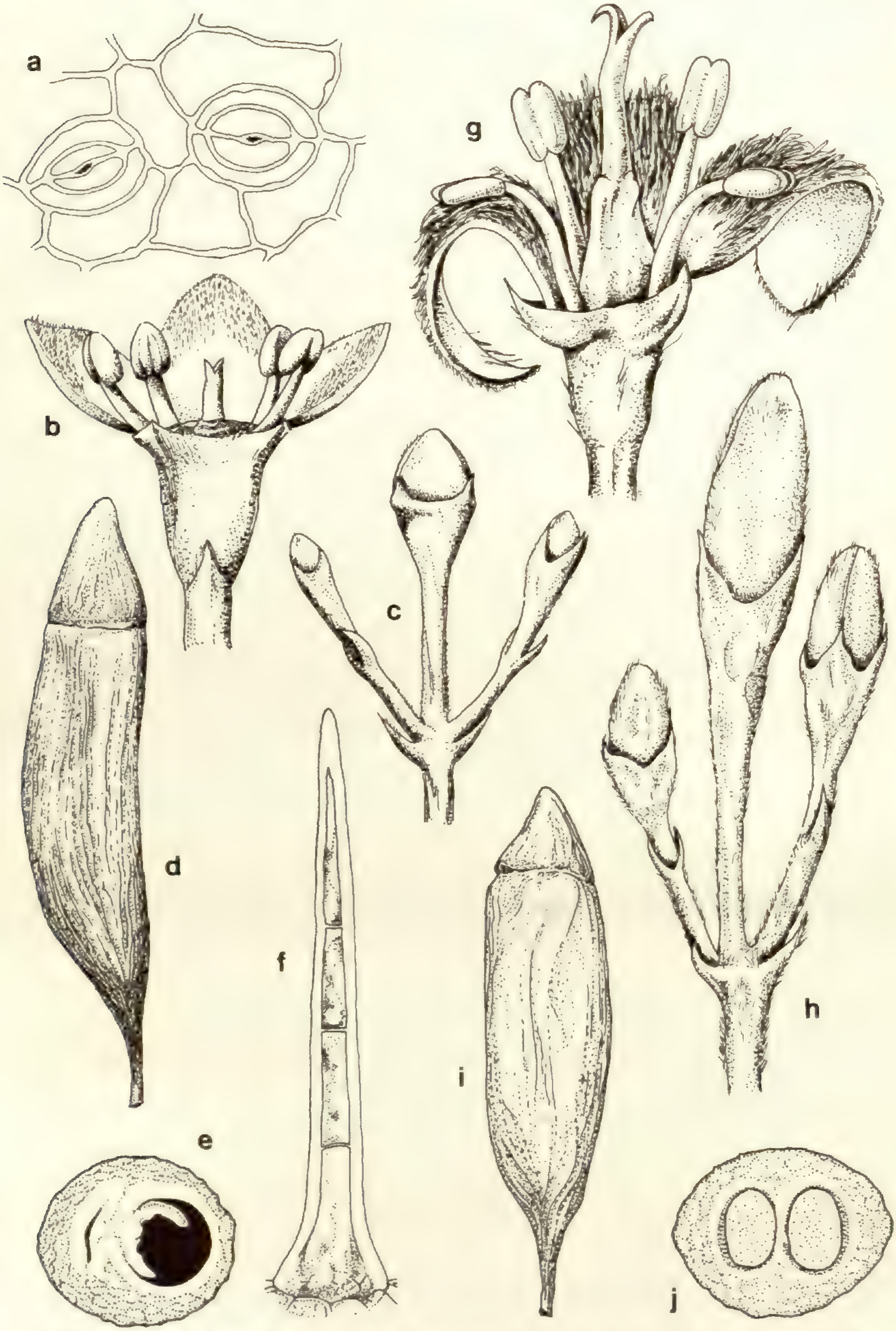


FIGURE 14. a–e, *Mastixiodendron flavidum*: a, view of abaxial surface of leaf blade showing pair of stomata, × 500 (from *A. C. Smith 6365*); b, flower with one corolla lobe removed, × 10 (from *A. C. Smith 6365*); c, dichasium with flower buds, × 8 (from *Fiji Dept. Agr. 15242*); d, fruit, × 2 (from *A. C. Smith 1790*); e, same in cross section, showing developed and aborted seeds, × 3. f–j, *Mastixiodendron pilosum*: f, trichome from abaxial surface of leaf blade showing relatively thick wall and thinner partitions, × 300 (from *H. B. R.*

with minute, scattered hairs about 0.2 mm. long, the costa conspicuous, plane to prominulous above, raised and rounded beneath, the secondary nerves 7 to 12(to 15) per side, prominulous above and beneath, the tertiary nerves and veinlets prominulous to plane above and beneath; inflorescences puberulent with scattered, minute hairs, delicate, open, with 1 or 2 (rarely 3) orders of branching and as many as 70 flowers, 4–10.5(–15) × 2.5–9.5 cm. at anthesis, 6–17 × 4–14 cm. in fruit, the peduncles slender, (2–)4–9 cm. long, to 1.5 mm. in diameter, the inflorescence bracts deciduous, deltoid, to 1.5 × 0.8 mm., obtuse to acute at apex, often clasping at base, sometimes erosulous at margin; pedicels slender, 1–3(–5) mm. long; calyx limb cupular, 1.5–2.5 mm. across, the lobes membranaceous, deltoid, 0.3–0.8(–1.2) mm. long, 0.5–1 mm. broad, obtuse to acuminate at apex, united at base into tube about 0.2 mm. high, glabrous to almost imperceptibly puberulent outside; corolla limb about 4 mm. across, the lobes white to orange to pale yellow, ovate to suborbicular, 1.5–2.5 mm. long, 1.5–2 mm. broad, obtuse to acute at apex, glabrous to finely puberulent outside with a few scattered hairs, densely puberulent to papillate distally inside with minute, yellow hairs about 0.1 mm. long, glabrous toward base; filaments of stamens 0.8–1 mm. long, about 0.2 mm. broad at base, tapering toward apex, the anthers about 0.5 mm. long, 0.3–0.5 mm. broad; inferior portion of ovary 1–1.5 × 1–1.5 mm., the disc broadly rounded, to 0.4 mm. high, glabrous; style caducous, 0.5–0.8 mm. long, about 0.3 mm. in diameter, truncate or divided about 0.2 mm. at apex; fruits green to yellow to orange, drying red-brown to nearly black, glabrous and often glaucous, broadly fusiform to long-obovoid, sometimes oblique, 20–32 × 6–8(–11) mm., tapering at both ends, the perianth scar 2–8 mm. below apex, the mesocarp thin, fleshy, the endocarp woody to coarsely fibrous, to 2 mm. thick, without conspicuous resin cavities; seeds about 12 × 3 mm., dark orange-yellow, wrinkled when dry.

NOMENCLATURE. Seemann based his description of *Canthium flavidum* on his own (flowering) collection, number *256*, cited below. The locality given on the holotype is "Matuata" (Mathuata, Vanua Levu), while that on the isotypes is Fiji, without further locality. The type of *Dorisia rarissima* is *Greenwood 517*, the collection on which Gillespie based his description, and known only from the holotype. It is a flowering specimen gathered near Lambasa (Mathuata, Vanua Levu) September 17, 1922, from a tree about 6 meters high growing at the edge of a clearing at an altitude of about 150 meters.

DISTRIBUTION AND ECOLOGY. *Mastixiodendron flavidum* is endemic to Fiji, where it has been collected on the islands of Viti Levu, Vanua Levu, and Rambi, and at altitudes from near sea level to about 1000 meters.

Parham III); g, flower with one corolla lobe removed, × 10 (from *Fiji Dept. Agr. 17094*); h, dichasium with flower buds, × 8 (from *Fiji Dept. Agr. 17094*); i, fruit, × 2 (from *A. C. Smith 6781*); j, same in cross section showing two developed seeds, × 3.

Isolated individuals are encountered in a variety of habitats, from high, dense, montane forests to dry, open, coastal forests and thickets. Flowering and fruiting specimens have been gathered throughout the year.

LOCAL NAMES. "Tembatemba" and "tuva ni viti" (Viti Levu), "reiova" (Vanua Levu), "kauloa" (Parham, 1972, cited above).

Fiji. VITI LEVU. MBA: Mt. Evans Range between Mt. Vatuyanitu and Mt. Natondra, *A. C. Smith 4368* (A, BISH, K, L, NY, US); vicinity of Nandarivatu, *Degener & Ordonez 13579* (A, BISH, K, L, NY, SUVA, US), *Gillespie 3870* (BISH), *A. C. Smith 5742* (A, BISH, BRI, K, L, NY, US); Navai Tea Block, *Fiji Dept. Agr. 14978* (BISH, BRI, K, LAE, SUVA); Mt. Tomanivi, *Lam 6845* (L). NANDRONGA & NAVOSA: Rairaimatuku Plateau between Nandrau and Nanga, *A. C. Smith 5561* (A, BISH, BRI, K, L, NY, US); Nandevondevo, near Vanualevu, *Fiji Dept. Agr. 1183* (BISH, SUVA). SERUA: coastal strip near Ngaloa, *A. C. Smith 9690* (BISH, GH, K, L, NY, SUVA, UC, US). NAMOSI: Mt. Vakarongasiu, *Fiji Dept. Agr. 16128* (L, SUVA). VANUA LEVU. MATHUATA: Nasealevu, Sasa, *Fiji Dept. Agr. 15242* (A, BRI, K, MASS, NY, SUVA, UC); southern slopes of Mt. Numbuiloa, east of Lambasa, *A. C. Smith 6365* (A, BISH, K, L, NY, US), *A. C. Smith 6444* (A, BISH, BRI, K, L, NY, US); vicinity of Lambasa, *Greenwood 517* (K, holotype of *Dorisia rarissima*); Mathuata, without further locality, *Seemann 256* (K, holotype of *Canthium flavidum*; isotypes at BM, GH). THAKAUNDROVE: Yanawai River region, Mt. Kasi, *A. C. Smith 1790* (BISH, GH, K, NY, US); mountains between Waiwai and Lomaloma, *Horne 608* (K); Vunimoli, Vaturamulo, *Fiji Dept. Agr. 15396* (BISH, LAE, SUVA); track to Mt. Nasorolevu, Savusavu, *Fiji Dept. Agr. 17141* (BISH, K, SUVA); Mt. Mariko, *A. C. Smith 430* (BISH, GH, K, NY, US); hills west of Korotasere, *A. C. Smith 1932* (BISH, GH, K, NY, US). RAMBI: mountains of Rambi, *Horne 441* (K).

The present species is reasonably distinct in its delicate branchlets, relatively small leaves, and open inflorescences. The flowers are the smallest of the genus, the corolla lobes are papillate to finely pubescent on their inner surfaces, and the discs are broad and glabrous.

The closest relative of *Mastixiodendron flavidum* is evidently *M. pilosum*; indeed, the fruits of those two taxa are hardly distinguishable. *M. pilosum* differs primarily in the lower surfaces of its leaf blades, which are persistently pubescent rather than glabrous, and in the longer flower buds, corolla lobes, stamen filaments, styles, and discs. However, in spite of those distinctions, a close relationship between *M. pilosum* and *M. flavidum* is further suggested by at least one collection (*Fiji Dept. Agr. 15242*) in which the relatively large leaf blades are pubescent, although the inflorescences and flowers are like those of *M. flavidum*. Another fruiting collection (*Fiji Dept. Agr. 15396*) has chartaceous and exceptionally large leaf blades, but because they are glabrous I have assigned it to the present species; it may represent material collected from sucker shoots.

The relationship of *Mastixiodendron flavidum* to *M. robustum* also seems close (as suggested by pollen morphology), although the flowers and fruits of the latter species are of a much larger size and an entirely different shape. In a few collections (e.g., *A. C. Smith 9690*), the leaf blades are thickly coriaceous and the branchlets particularly robust, although the

inflorescences and flowers appear to me to be definitely of the *M. flavidum* type.

7. **Mastixiodendron pilosum** A. C. Sm., Jour. Arnold Arb. **26:** 109. 1945, *op. cit.* **34:** 99. 1953; J. W. Parham, Pl. Fiji Isl. 198. 1964, ed. 2. 278. 1972. FIGURES 5; 14, f–j.

Slender tree to 10 m. high, the bole relatively short, to 75 cm. d.b.h.; branchlets 2.5–4(–6) mm. broad toward apex, red-brown to brown, densely puberulent when young; mature stipules broadly subulate to lanceolate, 17–24 × 3–6 mm., acuminate at apex, glabrous or finely puberulent with a few scattered hairs; petioles semiterete to subterete and somewhat canaliculate, 20–40 mm. long, 1.5–2.5 mm. broad, densely to finely puberulent with scattered hairs; leaf blades subcoriaceous to chartaceous, elliptic to oblong, (9–)12–24 cm. long, (3.5–)5–14 cm. broad, obtuse to rounded and bluntly cuspidate at apex, often somewhat revolute at margin, glabrous and glossy to glaucous above, pilose to tomentulose beneath with scattered, spreading, brown to stramineous hairs to 0.7 mm. long, the costa conspicuous, plane to raised and canaliculate above, raised and rounded beneath, the secondary nerves 8 to 11 per side, prominulous above, raised and rounded beneath, tertiary nerves and veinlets prominulous above and beneath; inflorescences puberulent with minute, scattered hairs, delicate, open, with 1 to 3 orders of branching and 25 to 55 flowers, 10–14 × 2–8 cm. at anthesis, 10–15 × (6–)8–11 cm. in fruit, the peduncles slender, subterete, 2.5–7 cm. long, 1–1.5 mm. in diameter, the inflorescence bracts caducous, deltoid to lanceolate, to 1.5 mm. long, to 0.5 mm. broad, acuminate at apex, often somewhat clasping at base; pedicels slender, 1–3(–5) mm. long; calyx limb cupular, 1.5–2.5 mm. across, the lobes coriaceous, deltoid, (0.5–)1–1.5 mm. long, 0.5–1 mm. broad, acute to acuminate at apex, united at base into shallow cup to 0.5 mm. high, puberulent outside with scattered hairs; corolla limb about 8 mm. across, the lobes yellow, long-elliptic to lanceolate, 4–4.5 mm. long, 1.2–1.8 mm. broad, puberulent outside with scattered hairs, densely puberulent distally inside with yellow hairs to 0.5 mm. long, glabrous toward base; filaments of stamens 1–2 mm. long, about 0.2 mm. broad at base, tapering toward apex, the anthers about 0.8 × 0.5 mm.; inferior portion of ovary 1.5–2 × 1–1.5 mm., the disc subconical, about 1.5 mm. high, blunt at apex, glabrous; style 1.5–2 mm. long, about 0.3 mm. in diameter, truncate to somewhat thickened at apex, not divided; fruits dull yellow to orange, drying dark orange to nearly black, glabrous, broadly fusiform to long-obovoid, sometimes oblique, 25–32 × 6–9 mm., usually tapering at both ends, the perianth scar 4–6 mm. below apex, the mesocarp thin, fleshy, the endocarp woody to coarsely fibrous, to 0.3 mm. thick, not especially resinous; seeds 8–13 × 1.5–2 mm., red-brown, glabrous.

NOMENCLATURE. The type of *Mastixiodendron pilosum* is *Horne 1132*, collected from a tree in a dry forest, September, 1878. The locality given

on the holotype is Fiji, without further information; the isotype reads "District of Bua [Mbua], Vanua Levu."

DISTRIBUTION AND ECOLOGY. Endemic to Fiji; collected on the islands of Viti Levu and Vanua Levu. *Mastixiodendron pilosum* occurs in dry, dense forests at altitudes from near sea level to 250 meters. Flowers and fruits have been gathered between the months of September and January. The wood is said to be hard, close-grained, and durable.

Fiji. VITI LEVU. NAMOSI: Wainandoi River valley, *Fiji Dept. Agr. 17094* (BISH, BRI, K, SUVA). VANUA LEVU. MBUA: between Mbua and Ndevoka, *H. B. R. Parham III* (A); Mbua, without further locality, *Horne 1132* (GH, holotype; isotype at K). MATHUATA: southern base of Mathuata Range, north of Natua, *A. C. Smith 6781* (A, BISH, BRI, K, L, NY, US).

The type collection of *Mastixiodendron pilosum* bears immature fruits which are essentially identical with those of *M. flavidum*. However, the leaf blades are generally larger, chartaceous rather than coriaceous, and bear a persistent indument on the lower surfaces. The petioles and young branchlets are also pubescent. Gillespie (1933) aligned the type collection with *M. flavidum*, but Smith (1945, cited above) segregated it and one other fruiting collection as *M. pilosum*, based primarily on the indument characters just mentioned. Since the first description of *M. pilosum*, specimens with immature and mature flowers have become available which strongly support the recognition of the present species as distinct from *M. flavidum*. The flowers of *M. pilosum* differ in their long-ellipsoid rather than subglobose buds, their longer corolla lobes puberulent on the inner surfaces with longer hairs, and their longer stamen filaments and styles. The discs are also subconical, instead of rounded, as in *M. flavidum*, and are similar in shape to those of *M. smithii* (although in numerous other characters of flowers and fruits the latter species is quite different).

The relationship of the present species with *Mastixiodendron robustum* would seem remote on the basis of floral and vegetative morphology, the latter species differing in its more thickly coriaceous leaf blades, more robust branchlets, and fewer-flowered inflorescences with larger, differently shaped flowers, among other more technical characters. However, as mentioned previously, a similarity in pollen morphology indicates that the three Fijian species (*M. robustum*, *M. flavidum*, and *M. pilosum*) are in fact closely related, as is also suggested by a few collections which are intermediate in their vegetative characters both between *M. robustum* and *M. flavidum*, and between *M. flavidum* and the present species.

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collections available (abbreviations after Holmgren & Keuken, 1974): A, BISH, BM, BRI, CANB, GH, K, L, LAE, MASS, MO, NY, SUVA, UC, US. Wood specimens were obtained from the Harvard Wood Collection.

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A REVIEW OF CORYLOPSIS (HAMAMELIDACEAE)

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AN EXAMINATION OF HERBARIUM MATERIAL and cultivated representatives of *Corylopsis* suggests that species have been named indiscriminately on the basis of incomplete specimens and an inadequate knowledge of variation within the genus. The fact that leaves of species of *Corylopsis* appear only after the flowers have fallen makes it necessary to gather two collections for every complete herbarium specimen. This situation, as well as the variability of the genus in China, has reduced parts of the taxonomy of these plants to a state of confusion.

To date, 33 species of *Corylopsis* have been described. All are shrubby plants valuable for their fragrant, yellow-flowered inflorescences borne on leafless twigs in early spring in the Northern Hemisphere. The genus has a distribution extending from the Himalayas in Bhutan, through Assam, across China, and into Taiwan and Japan; a species has also been described from Korea. For the distribution of the species recognized in this treatment, reference should be made to FIGURE 1.

Corylopsis occurred in the Boreal-Tertiary angiosperm flora (Takhtajan, 1969), having been found in Tertiary fossil beds, and the genus is also known from the London Clay flora of the early Eocene (Takhtajan, 1969).

At the present time, it is possible to recognize a Himalayan and a Chinese group of phenotypes, but upon closer analysis there is intergradation between the two divisions in areas such as Yunnan Province. The Chinese group can be subdivided further into a continental and an offshore group, the latter being found in Japan and Taiwan. The continental taxa are in general less morphologically distinct from one another than are the offshore taxa, which include species such as *Corylopsis spicata* Sieb. & Zucc. and *C. pauciflora* Sieb. & Zucc. At the same time, there are similarities between the continental and offshore species. A description of anthesis and a summary of the published cytological data available for the genus is given below, together with a new classification and a key to the species.

ANTHESIS

The spatial arrangement of petals, stamens, stigmas, and nectaries in *Corylopsis* flowers has received much attention from taxonomists, but it may be equally if not more useful to an understanding of the breeding system of the plants than it is to their taxonomy and relationships. The following observations show how the spatial arrangement of floral organs changes with time, and how an herbarium-based taxonomic study may relate to any one of a number of stages seen during the maturation of the inflorescence.

Several tightly imbricated inflorescence bracts protect the flowers during winter. Pollen is formed during the preceding August and September.

FIGURE 1. Distribution of *Corylopsis* species: 1, *C. pauciflora*; 2, *C. henryi*; 3, *C. multiflora*; 4, *C. himalayana* var. *himalayana*; 5, *C. himalayana* var. *griffithii*; 6, *C. spicata*; 7, *C. glabrescens*; 8, *C. sinensis* var. *sinensis*; 9, *C. sinensis* var. *calvescens*.

The inflorescence bracts are shed in February and March, exposing the flower buds, which are protected further by floral bracts that may or may not be hairy. As the floral bracts gradually expose each flower (FIGURE 2, a), the five yellow petals begin to part and expand, allowing the two styles to protrude from the flower. By this time the stigmas are receptive. In cultivation, styles at the same developmental stage protrude most from flowers of *Corylopsis glabrescens* Fr. & Sav. and least from those of *C. platypetala* Rehder & Wilson var. *levis* Rehder & Wilson (= *C. sinensis* var. *calvescens*) (see FIGURE 2, b). At this point the anthers have not dehisced and are borne on filaments shorter than the styles. Except for *C. veitchiana* Bean, now recognized as a form of *C. sinensis* var. *calvescens*, this dichogamous condition was found in all cultivated corylopses examined, and for the majority, this stage represents protogyny of the flowers.

The anthers dehisce only when the petals are fully expanded and the nectaries are revealed, at which time filament elongation has brought the

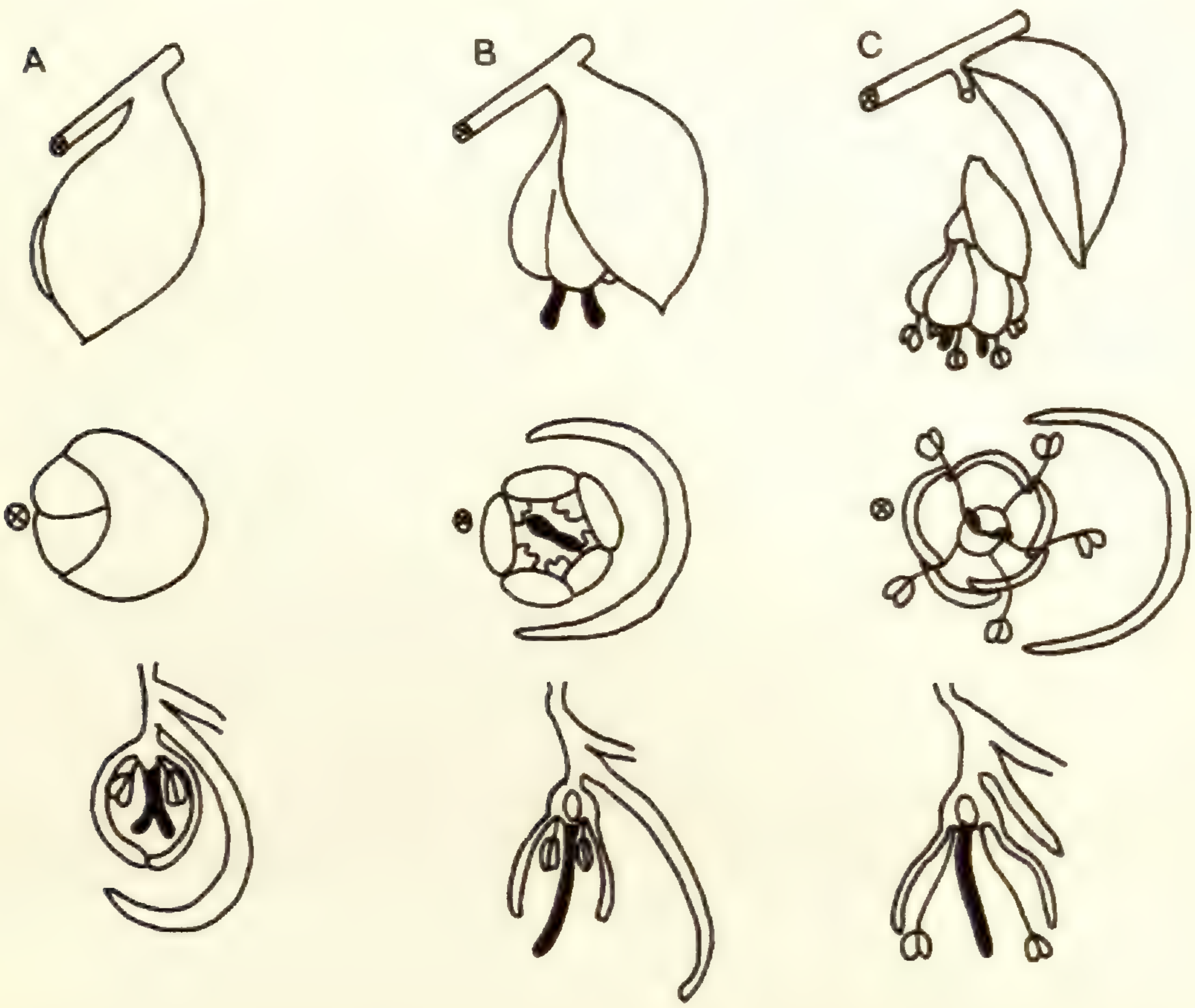


FIGURE 2. Anthesis in *Corylopsis*. Flowers shown from side, from below, and in section: a, unopened; b, stigmas exserted; c, fully open.

anthers to a level with or above the stigmas (FIGURE 2, c). Anther dehiscence and senescence is not always simultaneous within any one flower. Partial dichogamy is evident, since at this stage an inflorescence may bear flowers in phases a, b, or c, as shown in FIGURE 2, and geitonogamy is observed to occur by the activity of feeding insects such as honey bees, blowflies, and hover flies. Finally, all of the flowers are functionally hermaphroditic, and in the final stages of anthesis the floral organs begin to wither, the fruits begin to develop, and the leaves begin to expand.

As stated by Faegri and van der Pijl (1971), protogyny may be efficient as a measure against selfing if the stigma is receptive for only a matter of hours before the anthers dehisce, because after any allogamous pollen has germinated on the stigma there is almost immediate competition for ovules. In *Corylopsis*, where each ovary has only two ovules, prevention of selfing would seem to be almost assured by the partial dichogamy observed to extend over a period of at least 24 hours.

In cultivation at Glasnevin, *Corylopsis platypetala* (= *C. sinensis* var. *calvescens*) appears to flower earlier than *C. willmottiae* Rehder & Wilson

(= *C. sinensis* var. *sinensis*), as indicated in HISTOGRAM 1. Furthermore, microclimatic differences cause different flowering times on different parts of the same plant (see data for *C. gotoana* (= *C. glabrescens*) in HISTOGRAM 1). It follows that if this behavior is also found in nature (there is no reason to suppose that it does not), we may speculate that selfing on a shrub could take place until sufficient numbers of neighboring plants come into flower, at which time outcrossing could occur. Such a breeding system, together with polyploidy, helps to explain some of the complex variation patterns found in wild corylopses.

The flowers of most *Corylopsis* species appear to be adapted for allogamy on the basis of floral mechanism and size of genitalia, but as Stebbins (1970) notes, autogamy is often associated with reduction of flower size, and the smaller-flowered *C. himalayana* Griffith and *C. manipurensis* Hemsley (= *C. himalayana*) may prove to be autogamous. In these Himalayan taxa the stigmas are noticeably shorter in relation to petal length than is the case with the corresponding relationships of Chinese and Japanese taxa.

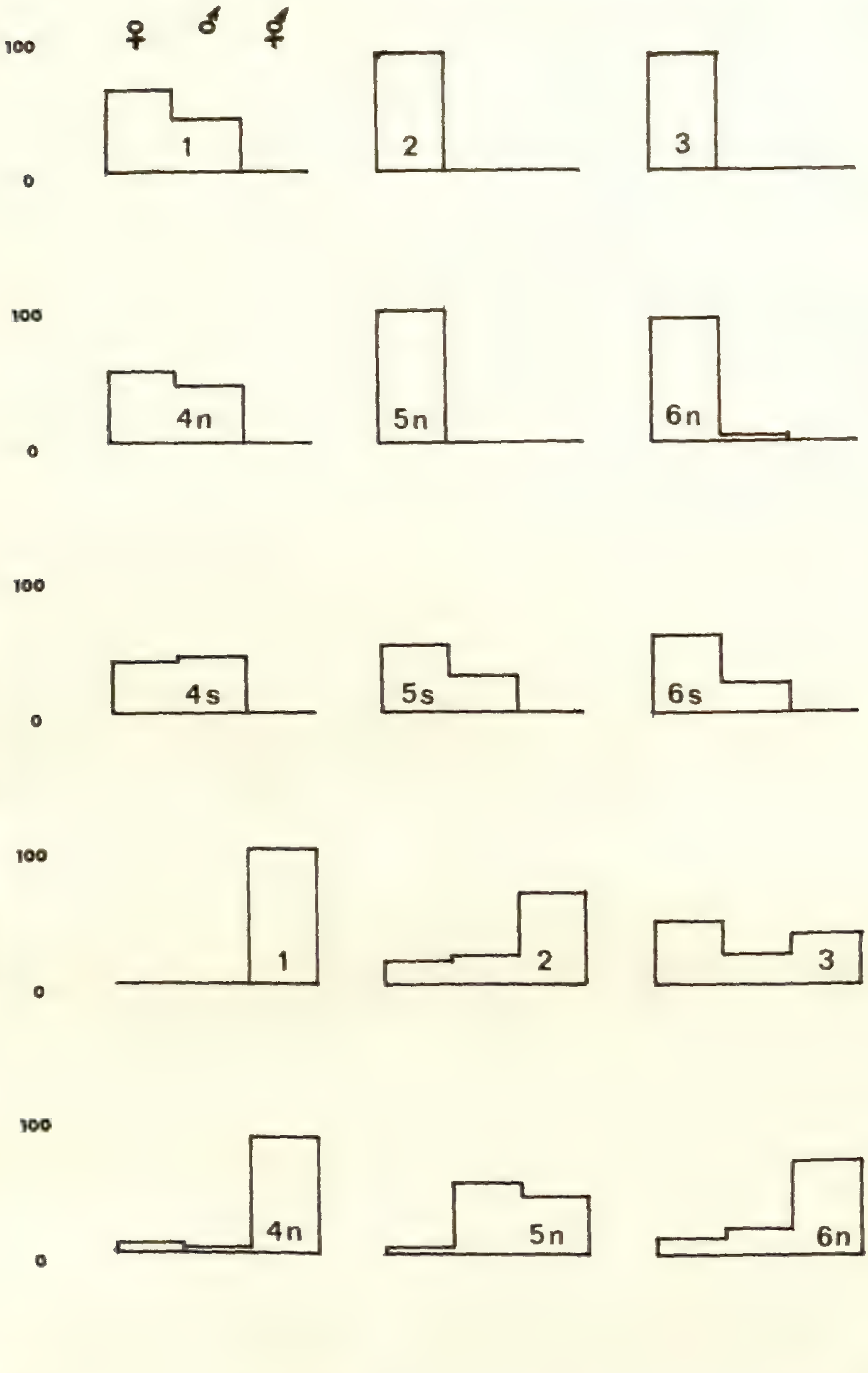
As shown in HISTOGRAM 2, all cultivated corylopses, with the exception of *Corylopsis pauciflora*, have roughly the same proportion of functionally female and hermaphroditic flowers at equivalent stages during anthesis, regardless of when flowering begins. There is no trend toward dicliny, as is found in the related genus *Sinowilsonia* Hemsley. Moreover, the absolute number of flowers in an inflorescence partly determines the duration of flowering.

An air frost of 2° C. for one night in 1972 killed the flower buds of *Corylopsis veitchiana* (a form of *C. sinensis* var. *calvescens*), but not those of *C. spicata*, *C. glabrescens*, or *C. platypetala* (= *C. sinensis* var. *calvescens*), which at Glasnevin were all similarly exposed. Fruits containing fertile seeds are regularly found on cultivated plants from September to December, so that the observed visits by pollen vectors seem to be pollination visits. Corylopses are insect pollinated in cultivation, but observations in nature are lacking. The flowers do not seem specialized for visits by any particular type of insect, and both dipterans and hymenopterans have been seen visiting the flowers to obtain the secretions from the nectaries.

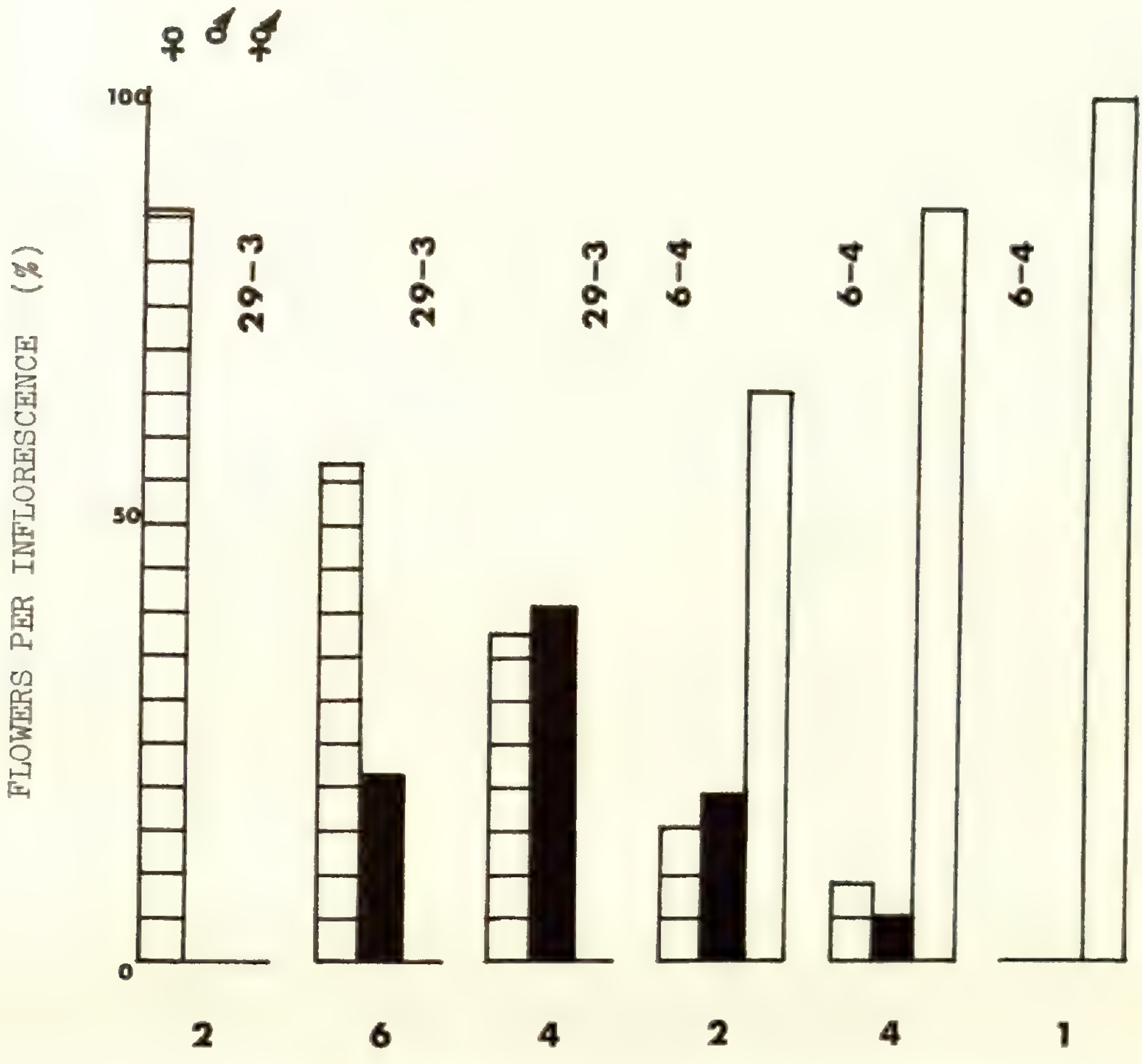
FLOWERS AND ANTHESIS IN RELATED GENERA

The relationship between the floral morphology and anthecology of *Corylopsis*, *Fortunearia* Rehder & Wilson, and *Sinowilsonia* require further study because the Chinese genera seem to illustrate stages in an evolutionary sequence from the hermaphroditic, entomophilous flower in *Corylopsis* to a unisexual (entomophilous?) one in *Sinowilsonia*. TABLE 1 shows some morphological differences between the three genera.

As noted above, the floral biology of *Corylopsis* is adapted to entomophily and outcrossing, with conspicuous nectaries, broad petals, and long stamens in the majority of species. Flowers appear before the leaves, thus



HISTOGRAM 1. Changes in functional sexuality of inflorescence during anthesis in selected *Corylopsis* species: 1, *C. spicata*; 2, *C. glabrescens*; 3, *C. willmottiae*; 4, *C. platypetala*; 5, *C. gotoana*; 6, *C. sinensis* (all cultivated at Glasnevin; n = north-facing twigs, s = south-facing twigs).



ABSOLUTE NUMBERS OF FLOWERS PER INFLORESCENCE

	flower number	sample
C. pauciflora	2	7
C. spicata	5-10	22
C. platypetala	9-16	150
C. yunnanensis	5-18	104
C. sinensis	6-18	129
C. willmottiae	11-18	118
C. glabrescens	10-21	98
C. platypetala var. levis	12-22	171
C. gotoana	12-22	149
C. veitchiana	15-30	161

HISTOGRAM 2. Summary of changes in functional sexuality of the inflorescence of *Corylopsis* (species as numbered in HISTOGRAM 1).

TABLE 1. **Differences between Corylopsis, Fortunearia, and Sinowilsonia.**

Character	Corylopsis	Fortunearia	Sinowilsonia
INFLORESCENCE	Axillary racemes on short shoots	Terminal racemes	Terminal and axillary racemes
SEX OF PLANT	Hermaphroditic, partial dichogamy	Andromonoecious	Unisexual; monoecious
SEPALS	Five small	Five small	Five spathulate
PETALS	Five large, ovate	Five subulate, equaling the sepals in length	Absent
STAMENS	Five with long filaments	Five almost sessile	Five with long filaments
DISC	Five bifid or truncate nectaries	Absent	Absent
HYPANTHIUM	Fused to ovary except in *C. henryi*, *C. brevistyla*, and *C. stelligera*	Fused to ovary	Free from ovary
FRUIT	Almost sessile	Stalked	Sessile

making the hermaphroditic and partially dichogamous inflorescences more conspicuous.

In contrast, the flowers of *Fortunearia* lack nectaries, have more inconspicuous, subulate petals as long as the sepals, and have almost sessile stamens and revolute styles; the stigmas come in proximity with the stamens. These attributes suggest a trend away from a pollination strategy like that of *Corylopsis*, with the development of andromonoecy. Some corylopses have attributes reminiscent of those of *Fortunearia*: the short stamens of *C. himalayana*, the truncate nectaries of *C. multiflora* (assuming that the truncate nectary is a reduction from the more common bifid condition in *Corylopsis*), and the elaboration of sexual phases in the raceme during anthesis. The male flowers of *Fortunearia* develop in autumn, are naked in winter, and have only a rudimentary ovary. Certain abortive *Corylopsis* flowers were found to have reduced stamens.

Sinowilsonia has diclinous flowers that lack nectaries and petals. The females possess five mucronate staminodes, but the males lack a vestigial gynoecium. Unlike most corylopses and *Fortunearia*, the ovary of *Sinowilsonia* flowers is not fused to the inner wall of the hypanthium, which almost completely encloses the ovary. Such a free ovary is also found in certain species of *Corylopsis*. The reproductive strategy in *Sinowilsonia* is

away from the showy displays that characterize *Corylopsis*. Outcrossing would be assured only by dichogamy of the separate sexes, for which no observations can be found. Alternatively, *Sinowilsonia* could be adapted to selfing by geitonogamy, but the development of unisexual flowers seems pointless when hermaphroditic ones can do the same job. It may be worth pointing out that *Sinowilsonia* is not andromonoecious as was stated by Sargent (1913); there are no hermaphroditic flowers, only ones with ovaries and staminodia.

CYTOLOGY

Hara (1972) described the polyploid differentiation of related species in Japanese and Sino-Himalayan species of *Aucuba* Thunb. and *Helwingia* Willd. The genus *Corylopsis* shares with these two genera a somewhat similar geographical distribution pattern, and available cytological data suggest that polyploid differentiation is parallel to the situation found in *Aucuba*, *Helwingia*, and other genera (see TABLE 2).

Apart from the fact that both *Corylopsis himalayana* and *C. pauciflora* are diploids and have quite distinctive and different phenotypes, there are no close correlations between the gross morphology of the plants and the chromosome number. As Anderson and Sax (1935) noted, "discovery [of polyploid series in *Fothergilla* and *Corylopsis*] is of . . . consequence since it indicates that in such genera we may expect . . . relationships between species which will be, in part at least, reticulate." Reticulate variation of morphological characters is common in the genus *Corylopsis*.

There is some relationship between published cytological and geographical data as far as the Japanese taxa are concerned, and more detailed work in Japan would help to clarify whether any meaningful evolutionary pattern exists. There is a lack of cytotaxonomic data for Chinese taxa; only the Himalayan *Corylopsis himalayana* has been examined cytologically. One might speculate that the large-leaved *C. himalayana* var. *griffithii* is a polyploid. The basic chromosome number for the genus seems to be $x = 12$.

TABLE 2. **Chromosome numbers in the genus Corylopsis.**

SPECIES	DISTRIBUTION	*n*	REFERENCE
C. himalayana	Himalaya	12	Mehra & Khosla, 1969
C. sinensis	China	12	Santamour, 1965
C. platypetala	China	12	Santamour, 1965
C. pauciflora	Japan	12	Anderson & Sax, 1935
C. pauciflora	Japan	12	Santamour, 1965
C. glabrescens	Japan	24	Santamour, 1965
C. willmottiae	China	24	Santamour, 1965
C. veitchiana	China	36	Anderson & Sax, 1935
C. veitchiana	China	36	Santamour, 1965
C. spicata	Japan	36	Anderson & Sax, 1935
C. spicata	Japan	36	Santamour, 1965

MORPHOLOGY

The following observations are based on examination of living plants at Glasnevin, Kew, and Mount Congreve Garden in Ireland, as well as from study of herbarium specimens from Kew, the British Museum (Natural History), Edinburgh Botanic Garden, Cambridge Botanic Garden, Wisley, the Arnold Arboretum and Gray Herbarium of Harvard University, U.S. National Herbarium, Smithsonian Institution, New York Botanical Garden, National Taiwan University, and Botanical Institute, Peking.

LEAF SHAPE. No significant differences in leaf shape were found in most of the cultivated taxa. The few exceptions, not in general cultivation, are *Corylopsis manipurensis* (= *C. himalayana*), with elliptical leaves having closely spaced veins, and *C. multiflora* Hance, which often has leaves with a conspicuously attenuate apex. The remaining taxa have ovate, obovate to orbicular leaf blades, the bases of which may be cuneate, oblique, or cordate.

The spacing of the nerves has an important, if in most cases taxonomically insignificant, effect on the appearance of the leaf. Spacing tends to be narrower on immature or poorly grown leaves. When closely spaced, the margin may appear serrate, as in *Corylopsis multiflora* or *C. polyneura* (= *C. sinensis*), or more characteristically sinuately dentate to denticulate, as in *C. manipurensis* (= *C. himalayana*), *C. spicata*, or *C. sinensis*. Protrusion of the veins beyond the leaf margin also determines the expression of margin elaboration, as for example when the leaves of *C. veitchiana* (= *C. sinensis* var. *calvescens* forma *veitchiana*) and *C. spicata* are compared. In certain specimens the leaves appear to have an entire margin because the teeth are revolute and the whole lamina is convex in profile; in cultivation this condition is seen in plants under water-stress or grown in exposed situations.

LEAF SIZE. The leaves of *Corylopsis pauciflora* rarely exceed 6 cm. in length; most other taxa have larger mature leaves to about 10 cm. Only *C. himalayana* var. *griffithii* has leaves regularly longer than 10 cm.

LEAF VESTITURE. The adaxial leaf surface is glabrous when mature, but when young it may be covered with an ephemeral sericeous indumentum of no taxonomic value. Such immature leaves may also appear glaucous or red-tinted in certain cultivated clones, i.e., *C. willmottiae* cv. Spring Purple (Hillier, 1974).

The abaxial leaf vestiture may persist until leaf-fall, and, in combination with inflorescence vestiture, it provides a useful character for identification of certain species. The petiole, and also the abaxial veins, may be tomentose, sericeous, sparsely glandular-hairy, glabrous and glaucous, or simply glabrous when mature; the petiole and vein vestiture appear to be linked characters. The lamina between the veins may be tomentose, sericeous, glabrous (and rough or smooth textured), or glabrous and glaucous, and while petiole and vein vestiture are normally correlated, that of the

lamina is not. This situation gives rise to a range of vestiture permutations, which are listed in TABLE 3.

The leaf vestiture of plants segregated as *Corylopsis trabeculosa* Hu & Cheng resembles that of *C. himalayana*, but the latter species does not always have the characteristic dense, rusty abaxial hairs shown in most specimens, e.g., *Gallatly 2775* (K!). Instead, the vestiture of *C. himalayana* can approach that of *C. sinensis*, with more of a colorless pubescence, as in *Cooper 1316* (K!) or *Gallatly 665* (K!).

INFLORESCENCE SIZE. The size of the inflorescence is a useful character to distinguish *Corylopsis pauciflora* from other taxa: it is short and consists of only one to five flowers. Other species tend to have inflorescences exceeding 5 cm. in length and containing more than five flowers. Apart from *C. pauciflora* and the synonymous *C. matsudai* Kanehira & Sasaki, all corylopses have catkin-like racemose inflorescences. *Corylopsis hima-*

TABLE 3. **Permutations of abaxial leaf vestiture in Corylopsis.**

TAXON	PETIOLE	VEIN	LAMINA
C. griffithii	T	T	T
	T	T	S
C. himalayana	T	T	GB
	S	S	T
	S	S	GB
C. multiflora	T	T	T
	T	T	GB
C. willmottiae	T	T	GB
	S	S	S
	S	S	GB
C. spicata	T	T	S
C. sinensis	S	S	T
	S	S	S
C. glabrescens	S	S	GB
C. pauciflora	S	S	GB
C. platypetala	S	S	GB
	GN	S	GB
C. yunnanensis	GB	S	S
C. manipurensis	GB	S	GB
C. glaucescens	GB	GB	GC
C. veitchiana	GB	GB	GB
C. glandulifera	GN	S	GB
C. hypoglauca	GN	GB	GC

T = tomentose-pubescent, S = sericeous, GB = glabrous, GC = glaucous, and GN = glandular.

layana and *C. manipurensis* (= *C. himalayana*) differ from the Chinese and Japanese species in having inflorescences with narrower petals and with flowers often more widely spaced apart on the rachis.

INFLORESCENCE VESTITURE. The hairs on the inflorescence can be divided into two categories: those on the rachis, and those on the bracts inserted on the rachis. TABLE 4 shows the condition(s) in the more commonly grown species. It is apparent that inflorescence vestiture is variable in taxa such as *Corylopsis sinensis*, but less so in *C. multiflora*. FIGURE 3 shows typical rachis bracts of *C. sinensis* and *C. himalayana*, as well as of intermediates collected by Augustine Henry (*5854*, K) and E. H. Wilson (*65*, K). The Henry material from Hupeh Province is, on the basis of other characters, best placed in *C. sinensis*, but in certain characters it approaches the variation seen in *C. himalayana* and *C. himalayana* var. *griffithii*. The same situation is found in *Schneider 753* (K), which is from southern Szechuan and is labeled *C. yunnanensis* (= *C. sinensis*). *Wilson 65* (K) shows further intermediate inflorescence vestiture between *C. sinensis* and *C. himalayana*.

FLOWERS. The vestiture of the floral organs is as variable as that of the vegetative ones. Thus, type material of *Corylopsis yunnanensis* (= *C. sinensis*) has a glabrous hypanthium and sepals (*Forrest 4095*), but *Schneider 2794* has a hirsute hypanthium. Type material of *C. willmottiae* (= *C. sinensis*) has a glabrous hypanthium and sepals (*Wilson 1316*), as does *McLaren 126*, but *Forrest 7252* has basally hairy hypanthia with sepals

TABLE 4. **Inflorescence vestiture in Corylopsis.**

	VESTITURE TYPE		
RACHIS	Tomentose-pubescent	Sericeous	Glabrous
	C. glabrescens *C. griffithii* *C. henryi* *C. himalayana* *C. manipurensis* *C. multiflora* *C. sinensis* *C. spicata* *C. willmottiae* *C. yunnanensis*	*C. glandulifera* *C. platypetala* *C. pauciflora* *C. sinensis* *C. veitchiana* *C. yunnanensis*	*C. glabrescens* *C. glaucescens* *C. hypoglauca* *C. henryi* *C. pauciflora*
FLORAL BRACTS	*C. griffithii* *C. henryi* *C. himalayana* *C. manipurensis* *C. multiflora* *C. sinensis* *C. yunnanensis*	*C. glabrescens* *C. glandulifera* *C. pauciflora* *C. platypetala* *C. sinensis* *C. spicata* *C. veitchiana* *C. willmottiae*	*C. glabrescens* *C. glaucescens* *C. henryi* *C. hypoglauca* *C. pauciflora* *C. spicata* *C. sinensis*

FIGURE 3. Rachis bracts: a–c, *C. sinensis* var. *sinensis* (a from *Ching 2598*, b from *Wilson 65*, c from *Henry 5854*); d, *C. himalayana* var. *himalayana* (*Griffith s.n.*, K). Bar scale = 1 mm.

fringed with hair at the margins. Material of *C. himalayana* (*Griffith s.n.*), from Bhutan, has a glabrous hypanthium and sepals, but other collections often show vestiture. The same can be said for specimens of *C. veitchiana* (= *C. sinensis* var. *calvescens* forma). The flowers may be discussed in terms of (a) the hypanthium or "calyx tube," (b) the nectaries, (c) the stamens, and (d) the petals.

HYPANTHIUM. Most corylopses have an ovary that is at least partly adnate to the inside of the hypanthium, but this is not so in *Corylopsis henryi*, *C. brevistyla* (= *C. henryi*), and perhaps *C. stelligera* Guillaumin (= *C. henryi*), all of which have more or less free ovaries. The hypanthium has several types of vestiture (see TABLE 5).

The majority of corylopses have conspicuous sepals, which may differ in shape from species to species. Thus, *Corylopsis spicata* has long leafy sepals, while *C. sinensis* has shorter, more fleshy ones. *Corylopsis multiflora*, including the synonymous taxa *C. wilsonii* and *C. cavaleriei* (see below), is notable for lacking free sepals.

TABLE 5. **Hypanthium vestiture in Corylopsis.**

SHORT PILOSE	PILOSE AT BASE	GLABROUS
C. griffithii	*C. glandulifera*	*C. glabrescens*
C. himalayana	*C. platypetala*	*C. glandulifera*
C. sinensis	*C. sinensis*	*C. glaucescens*
C. veitchiana	*C. spicata*	*C. henryi*
C. yunnanensis	*C. willmottiae*	*C. hypoglauca*
		C. himalayana
		C. multiflora
		C. pauciflora
		C. platypetala
		C. manipurensis
		C. spicata
		C. veitchiana
		C. willmottiae
		C. yunnanensis

NECTARIES. Only in *Corylopsis multiflora*, *C. wilsonii* (= *C. multiflora*), and *C. pauciflora* are the nectaries notably truncate and simple. In all other corylopses the nectaries are bifid, the tips being pointed or blunt. In some specimens of *C. glabrescens*, the nectaries are not the usual green color, but reddish. The nectaries are shiny and secrete a sweet fluid attractive to dipterans (*Calliphora erythrocephala* and *Melanostoma scalare*) and hymenopterans (*Apis mellifera*) at Glasnevin. The tips of the nectaries often bend at right angles away from the center of the flower.

STAMENS. Herbarium material does not facilitate study of the spatial relationships between the stamens, stigmas, and petals, relationships which have been shown above to change according to the age of the flower. As cultivated material is generally without known origin, it is important that field studies be carried out to determine the floral biology of as many of the wild species as possible. In particular, the lengths of the styles of Chinese and Himalayan taxa should be compared at the same stage of anthesis.

The filaments of most taxa are greenish when young and become yellow or whitish when mature, but in *Corylopsis spicata* they are often bright red. The anthers of most taxa are yellow before anthesis, but in *C. himalayana* var. *griffithii*, *C. spicata*, and *C. veitchiana* (= *C. sinensis* var. *calvescens* forma) they are reddish brown, while some plants of *C. sinensis* have orange anthers.

PETALS. Petal color is always yellow, but in *Corylopsis himalayana* it is often very pale yellow. The shape of the petals of different taxa has been used as a taxonomic character, but such action is partly responsible for the long synonymy in *Corylopsis*. Petal shape should be used only in conjunction with other characters in the delimitation of taxa. For example, the spathulate petals of *C. spicata* is one of a group of characters that distinguishes this species from *C. sinensis*, which has orbicular petals. Corylopses have clawed petals; in some species the length of the claw varies with age by a factor of three or four.

On the basis of herbarium study, petal size appears to distinguish *Corylopsis himalayana* and *C. manipurensis* (= *C. himalayana*) from Chinese taxa, the former possessing inflorescences that are not congested with open flowers like the Chinese taxa. Chinese material provides a greater amount of visual pollinator attraction; as a result, they are more valued horticultural subjects. Visual attraction is not as great in the Himalayan *C. manipurensis* (= *C. himalayana*), which has only one petal in each flower. On the basis of style length and overall flower size, *C. himalayana* and *C. manipurensis* (= *C. himalayana*) may be more autogamous than Chinese or Japanese plants.

The characters which appear to be taxonomically reliable are leaf size, leaf vestiture (for certain taxa), inflorescence length and vestiture, ovary–hypanthium adnation, absence of free sepals, nectary shape (bifid or truncate), stamen color (for some intraspecific taxa), and petal shape and

size. Because both types of characters are essential, it was found impossible to use only reproductive or only vegetative characters for the identification of corylopses.

PREVIOUS TREATMENTS

Many binomials in *Corylopsis* were established within a relatively short time at the beginning of the twentieth century, when availability of dried material and newly introduced cultivated material from the Far East was at a peak. The description of new taxa represents a slow, uncritical accumulation of information on the variation of these plants, and particularly the *C. sinensis* complex.

Chinese plant explorations enabled William Botting Hemsley (1843–1924) to describe six new taxa in 1906; his "Corylopseos specierum diversarum analyses" in Hooker's *Icones Plantarum* for that year included useful comparative references and illustrations of the species then recognized.

In 1930, Hermann August Theodor Harms (1870–1942) devised the first and only intrageneric classification of *Corylopsis*, recognizing the groups or sections HENRYANAE, MULTIFLORAE, PAUCIFLORAE, SPICATAE, and MANIPURENSES. This classification was based on whether the ovary is fused to the hypanthium or not, whether the sepals are conspicuous or not, petal number, and nectary shape and number. It is clear that Harms had a good appreciation of critical characters in *Corylopsis* so far as the more distinct species are concerned, but he failed to examine the relationships of the more phenotypically similar species. Consequently, his sect. SPICATAE is heterogeneous, containing such phenotypically diverse taxa as *C. spicata*, *C. glabrescens*, *C. stenopetala* (= *C. multiflora*), *C. sinensis*, and *C. himalayana*. His lack of awareness of the variation of *C. himalayana* led him to create a special section for *C. manipurensis* (= *C. himalayana*). To some extent he also contradicted his own classification by placing *C. stenopetala* (= *C. multiflora*) in sect. SPICATAE and not in sect. MULTIFLORAE.

TAXONOMY

Corylopsis Siebold & Zuccarini, Fl. Japon. 1: 45. 1835.

Deciduous shrubs, the branches initially stellate-pubescent; leaves petiolate, the blades ovate to orbicular, cordate to broadly cuneate or oblique at base, conspicuously nerved, the margin serrate to sinuately dentate or denticulate; stipules large and caducous; flowers precocious, usually in catkin-like racemes, axillary on short shoots, the inflorescence bracts concave, membranaceous, brown; floral bracts concave, less membranaceous than the inflorescence bracts, pale brown or transparent to greenish; sepals 5 or inconspicuous, the hypanthium usually adnate to the gynoecium; petals yellow, 5 (rarely reduced to 1), perigynous, clawed, obovate to spathulate; stamens 5, alternate with the 5 bifid or truncate nectaries, the anthers basifixed; ovary semi-inferior to superior, bilocular, styles slender, 2. stig-

mas small and capitate; 1 ovule in each ovary loculus; fruit a subglobose, bivalved, woody capsule, each valve bifid, the calyx normally persistent; seeds black, shiny, oblong-cylindrical, the testa hard. LECTOTYPE SPECIES: *C. spicata* Sieb. & Zucc.

KEY TO THE SPECIES OF CORYLOPSIS

1. Inflorescences with 1–5 flowers; leaves to 6 cm. long; plants diploid, of Japan and Taiwan. ..... 1. *C. pauciflora.*
1. Inflorescences with more than 5 flowers; leaves more than 6 cm. long at maturity.
   2. Ovary free from the hypanthium; floral bracts externally sericeous to glabrous when dry. ..... 2. *C. henryi.*
   2. Ovary fused to the hypanthium; floral bracts externally villose to sericeous when dry.
      3. Sepals apparently absent; nectaries truncate. ..... 3. *C. multiflora.*
      3. Sepals present; nectaries bifid.
         4. Floral bracts externally brown-villose when dry.
            5. Leaves to 10 cm. long; inflorescences 7–8 mm. in diameter, petals 5 or rarely reduced in number to 1. ..... 4. *C. himalayana* var. *himalayana.*
            5. Leaves more than 10 cm. long; inflorescences 10–12 mm. in diameter; petals 5. ..... 4a. *C. himalayana* var. *griffithii.*
         4. Floral bracts externally sericeous or rarely glabrous when dry.
            6. Sepals lanceolate and leafy; flowers often fewer than 10, clustered toward the tip of the rachis; plants hexaploid, of Japan. ..... 5. *C. spicata.*
            6. Sepals shortly ovate and fleshy; flowers often more than 10, distributed evenly along the rachis; plants diploid, tetraploid, or hexaploid, of Japan and China.
               7. Sepals bluntly triangular, about 1 mm. long; inflorescence ca. 8 mm. in diameter; flowers widely spaced on the glabrous rachis; leaves ca. 8 cm. long at most, the abaxial veins sericeous to glabrescent; plants tetraploid or hexaploid, of Japan and Korea. ..... 6. *C. glabrescens.*
               7. Sepals ovate to triangular, ca. 2 mm. long; inflorescence ca. 10 mm. in diameter; flowers closely spaced on a pubescent, sericeous, or glabrous rachis; leaves to ca. 12 cm. long, the abaxial veins pubescent or sericeous, or if rachis glabrous and glaucous, the veins glabrous.
                  8. Leaves with the abaxial lamina pubescent between veins, rarely glabrous, often roughly reticulate with pronounced secondary veins; petioles densely adpressed-pilose to tomentose, the rachis tomentose to coarsely pilose, rarely glabrous as in var. *calvescens*; plants diploid or tetraploid, of China. ..... 7. *C. sinensis* var. *sinensis.*
                  8. Leaves with the abaxial lamina glabrous between the veins, smooth with inconspicuous secondary veins; petioles glabrous to sparsely adpressed-pilose, sometimes glandular; plants diploid or hexaploid, of China. ..... 7a. *C. sinensis* var. *calvescens.*

1. **Corylopsis pauciflora** Sieb. & Zucc., Fl. Japon. 1: 48. *t. 20.* 1835; Hooker, Curtis's Bot. Mag. 126: *t. 7736.* 1900. HOLOTYPE: *Siebold s.n.* (L or LE), not seen.

Corylopsis Matsudai Kanehira & Sasaki, Trans. Nat. Hist. Soc. Formosa **20:** 383. 1930. HOLOTYPE: *Matsuda 12* (TAI!).[1]

Spreading, much-branched shrub to 3 m.; young shoots slender, glabrous; petiole 5–15 mm. long, glabrous; leaves ovate, 3–6.5 cm. long, acute at apex, cordate to subcordate at base, oblique, the margin sinuate-dentate with bristle-like, excurrent teeth; abaxial surfaces of the leaf blades glaucescent, sparsely sericeous on the 5 to 9 pairs of veins; inflorescence 2–3 cm. long, ca. 8–10 mm. in diameter, the rachis glabrous to sparsely sericeous and the bracts externally glaucous, glabrous, and reddish; flowers 1 to 5, yellow, the floral bracts externally glabrous to sericeous; sepals 2 mm. long, orbicular, glabrous; petals 7–8 mm. long, oblong-obovate; anthers pale yellow, the filaments yellowish; ovary fused to the glabrous hypanthium, the style yellowish, the 5 nectaries entire and truncate, shorter than the sepals; capsules glabrous, 6–8 mm. in diameter.

LOCAL NAMES. Hyūga-mizuki, Lyo-mizuki (Ohwi, 1965).

REPRESENTATIVE SPECIMENS. **Korea.** KYENGKI: Seoul, 1933, Smith, 9–30 (A). **Japan.** HONSHU: Mt. Kimiosan, *Murata 19245* (K); Komatsu-shi, *Takahashi s.n.* (A); Fuchu in Musashi, *Mizushima 1127* foliage = *1016* flowers (K, E); Mt. Oeyama in Tango Prov., *Togasi 1513* (K), *Tashiro 953* (E); Yokohama hort., *Bisset 1086* (BM, E, K); "Hondo," without further locality. *Wilson 6323* (K). KYUSHU: Nagasaki hort., *Maximowicz 10006* (BM), Nagasaki, *Maximowicz s.n.* (K), March, 1900, *Veitch s.n.* (K); Kyushu, without further locality, *Wilson 6230* (BM). **Taiwan:** Mokwazan, *Nakamura 4558* & *5248* (TAI); Tenchozen, *Matsuda 12* (TAI); Ching-sui Shan, *Shimizu & Kao 11736* (TAI).

Corylopsis pauciflora was introduced to Britain by Messrs. Veitch sometime prior to 1900; as their catalogues of the early 1900's indicate, their firm helped to make this species well known in gardens. According to Dr. Li (1962), Dr. G. R. Hall introduced the species to North America (Rhode Island) in 1874; Bretschneider (1898) pointed out that Robert Fortune made the first non-commercial introduction of the species to Britain in 1860–61, and also noted that a year later it was being grown in Leningrad after having been introduced there by Maximowicz.

A delicate little shrub which is still commercially available, *Corylopsis pauciflora* is suited for the small or shaded woodland garden, as it tends to become scorched when planted in dry or exposed situations, and chlorotic in limey soils. It is said to be less hardy than species such as *C. spicata* in the British Isles (see FIGURE 4). Field notes on *C. pauciflora* in Japan by Y. Shirosaki can be found in Jour. Jap. Bot. **28:** 95 (1953).

[1] The only collection cited by Kanehira and Sasaki as representing *Corylopsis Matsudai* was *Matsuda 21866. Ed.*

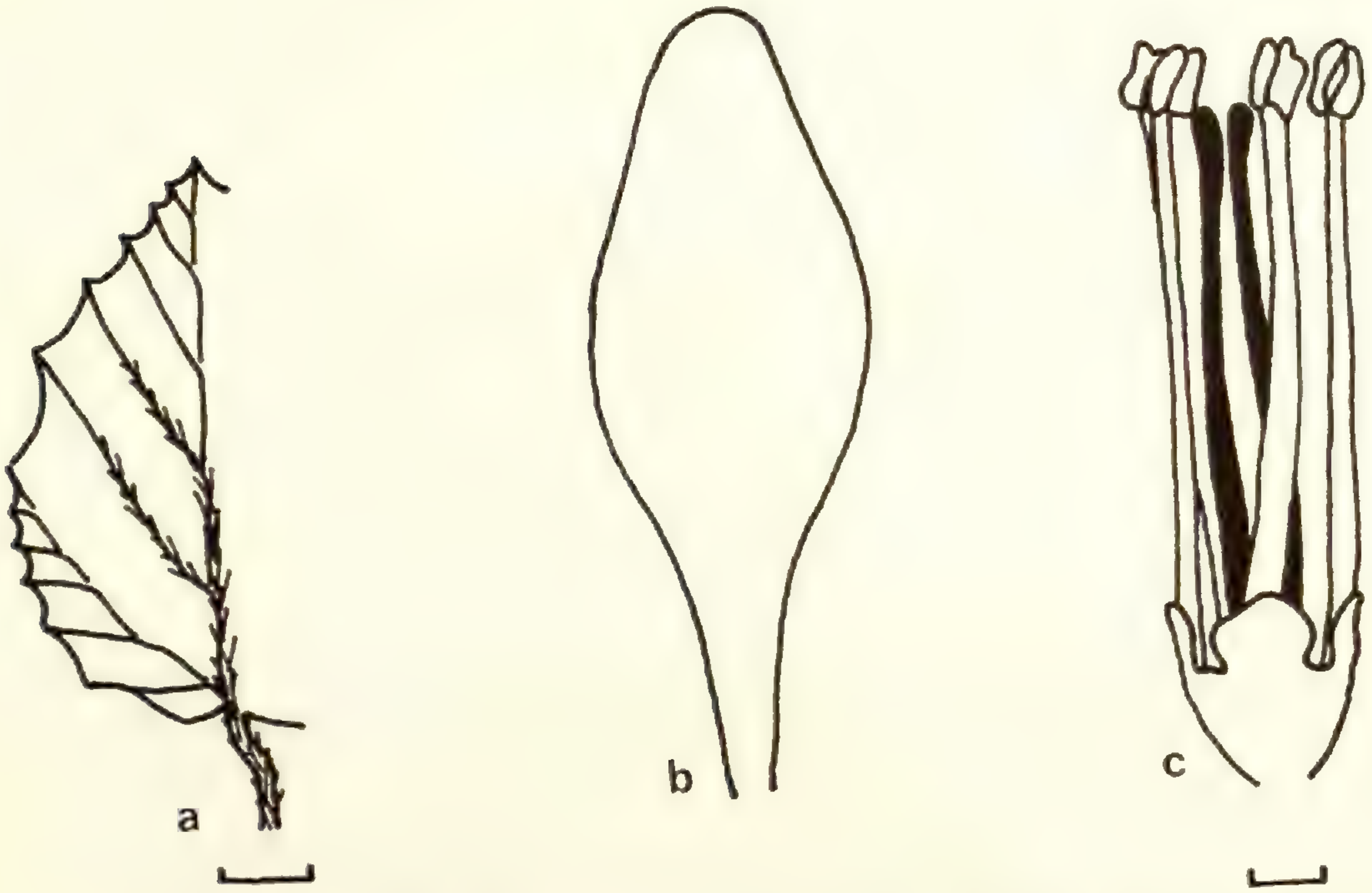


FIGURE 4. **Corylopsis pauciflora:** a, leaf profile showing abaxial vestiture (*Veitch s.n.*, type of Curtis's Bot. Mag. **126:** *t. 7736*); b, petal; c, flower lacking petals (flowers cultivated in Glasnevin as *C. pauciflora*). Bar scale by leaf in all cases = 1 cm.; bar scale for flowers, including petals, in all cases = 1 mm.

2. **Corylopsis henryi** Hemsley, Hooker's Icon. Pl. **29**: *tt. 2819, 2820.* 1906. HOLOTYPE: *Henry 1444* (K!).

Corylopsis stelligera Guillaumin, Bull. Soc. Bot. France **61**: 38. 1914; Lecomte, Not. Syst. **3**: 25. 1914. HOLOTYPE: *Farges 137* (P?), not seen.

Corylopsis brevistyla Chang, Sunyatsenia **7**: 71. 1948. ISOTYPES: *Maire 153* (BM!, E!).

Shrub to small tree with slender, glabrous shoots; leaves not seen in mature state; inflorescence ca. 4 cm. long, the rachis glabrous to villose; flowers 10 to 18, yellow, the bracts externally glabrous to villose; sepals ca. 2 mm. long, ovate-oblong, glabrous to pilose; petals 6–8 mm. long, spathulate to suborbicular; stamens not seen fresh; ovary free or only slightly fused to the glabrous or pilose hypanthium, the style not seen fresh, the nectaries 5, bifid, tips acute to obtuse, shorter than the sepals; capsules not seen.

REPRESENTATIVE SPECIMENS. **China.** HUPEH: Patung, *Henry 1444* (K). YUNNAN: Ho ki keou, *Maire 51037 (153)* (BM, E).

The floral structure of *Corylopsis henryi* is so distinctive that the species was described in the absence of mature leaves. *Corylopsis brevistyla* was also described only from flowering material; from written descriptions we see that it apparently has the free ovary character of *C. henryi.* It differs,

however, in having villose instead of subglabrous floral bracts and inflorescences, orbicular instead of spathulate petals, and bifid, blunt-tipped instead of sharply tipped nectaries.

While floral morphology seems to place *Corylopsis henryi* and *C. brevistyla* together, and the latter is tentatively placed in the synonymy of *C. henryi* here, more material is needed to determine their full relationship and the reliability of the free ovary character. *Corylopsis stelligera*, also here placed tentatively in the synonymy of *C. henryi*, reputedly differs from *C. henryi* (including *C. brevistyla*) in having an externally pilose hypanthium and exserted anthers. Although we have not seen type material (*Farges 137*, Sut-chuen, Tchen-keou-tin district) which consists of both flowers and fruits, the description states that the ovary and hypanthium are not adnate. Again, more material from the type locality of *C. stelligera* would improve our understanding of this taxon. *Corylopsis henryi*, as construed here, does not appear to have been introduced into cultivation (see FIGURE 5).

3. **Corylopsis multiflora** Hance, Ann. Sci. Nat. ser. 4. **15**: 224. 1861. HOLOTYPE: *Hance 6684* (BM!); isotype (K!).

Corylopsis wilsonii Hemsley, Hooker's Icon. Pl. **29**: *t. 2819*. 1906. HOLOTYPE: *Wilson 18* (K!); *isotype* (GH!).

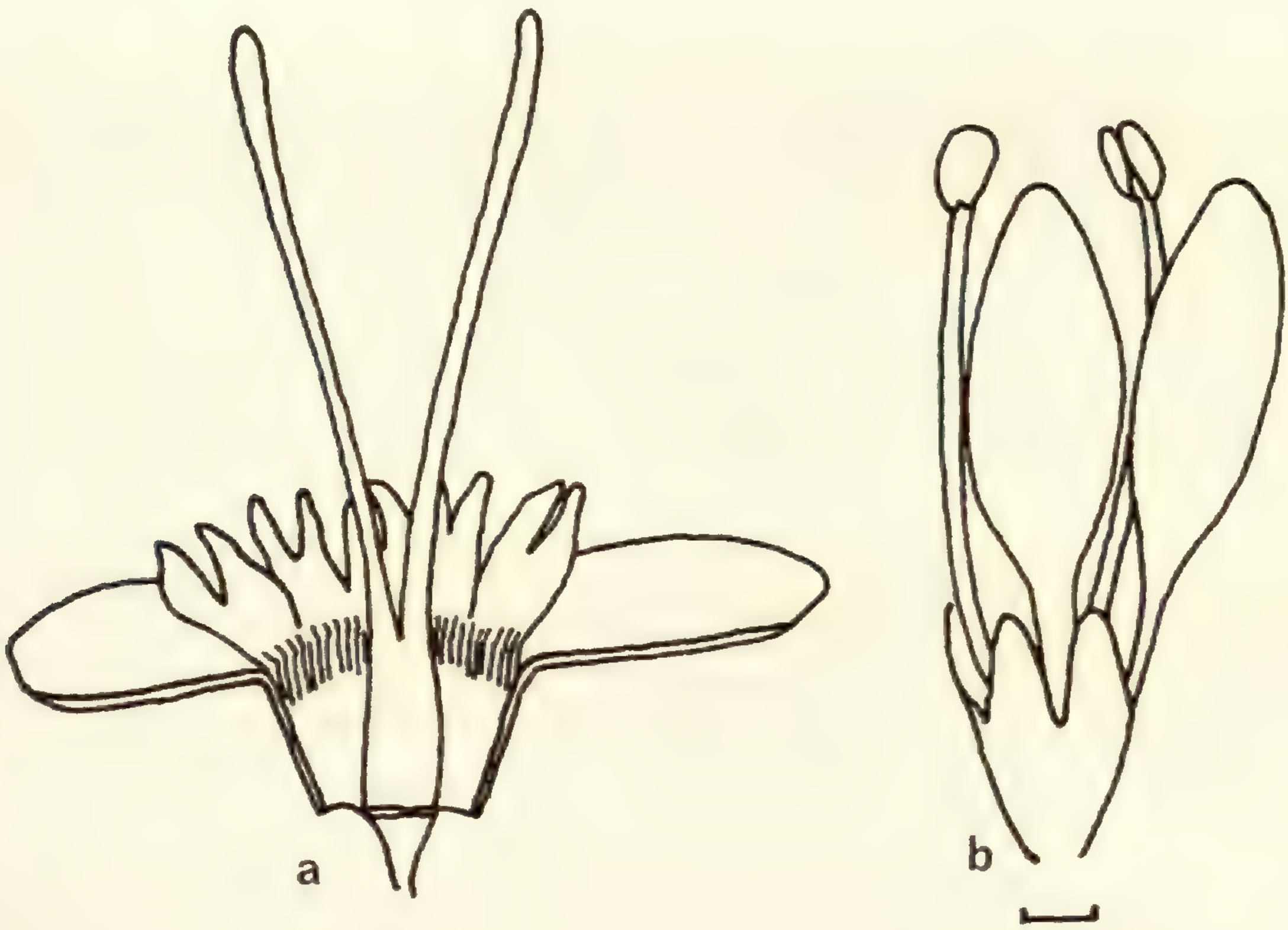


FIGURE 5. **Corylopsis henryi:** a, flower dissected to show free ovary; b, flower with two petals (a, b after Smith in Hooker's Icon. Pl. **29**: *t. 2820, figs. 15, 16,* originally drawn from the holotype, *Henry 1444*).

Corylopsis cavaleriei Léveillé, Feddes Repert. **11:** 295. 1912. ISOTYPES: *Cavalerie 1098* (E!, K!).

Corylopsis stenopetala Hayata, Icon. Pl. Formosa. **4:** 6. 1914. HOLOTYPE: *Ito s.n.* (TI), not seen.

Corylopsis cordata Merrill ex Li, Jour. Arnold Arb. **24:** 445. 1943. ISOTYPE: *Tsang 22261* (BM!).

Shrub or small tree with stellate-pubescent or villose young shoots; petiole 1–2.5 cm. long, densely pubescent to villose; leaves ovate to obovate, or ovate-lanceolate to elliptic, acute or caudate at tip, cordate to truncate at base, 7–15 cm. long, the margin sinuate-dentate with or without bristle-like, excurrent teeth; abaxial surfaces of the leaf blades glaucous and pubescent-tomentose, more rarely glabrous with villose veins or entirely glabrous, the veins in 6 to 9 pairs; inflorescence 2.5–7 cm. long, 1–1.3 cm. wide, the rachis pubescent to tomentose and the bracts externally pale brown-lanate; flowers 10 to 20, yellow, the bracts externally sericeous to pale brown and silvery-lanate; sepals inconspicuous; petals 5–6 mm. long, linear-spathulate; stamens not seen fresh; ovary fused to the glabrous hypanthium, the styles not seen fresh, the nectaries 5, entire, thick and truncate; capsule glabrous, 7–12 mm. in diameter.

REPRESENTATIVE SPECIMENS. **China.** FOKIEN: Ankoe, legit. de Grijs, *Hance 6684* (BM, K). KWEICHOW: Pin-fa, *Cavalerie 1098* (E, K); Pin-fa, Lofou, *Cavalerie 2927* (E, K); Pai Sha Chi, Fan Ching Shan, *Steward et al. 722* (BM, K); Sandjio, *Handel-Mazzetti 10797* (K). HUPEH: Patung, *Wilson 1781* (K), *Wilson 18 = 1166* (GH, K); Enshih Hsien, *Chow 1852* (E). KWANGTUNG: near Chengkou, *Chun 5820* (A, E, K); Pan Ling Tsze, *Chun 5855* (E); Lok Chong, *Tso 20516* (A); Shap Man Taai Shan, border with Shangtze, *Tsang 22261* (BM). KWANGSI: Pan-pu-ts'un, Pai Shou, *Ying-wah 73* (K); Lao Pao k'ou, *Steward et al. 1095* (A); Bin Long, *Ching 6038* (A).

Steward et al. 722, *Chun 5855*, and other specimens have notably glaucous undersides to the leaves.

Both *Corylopsis multiflora* and plants segregated as *C. wilsonii* by Hemsley have thick, truncate nectaries and lack conspicuous sepals; this fact may be seen in the illustrations in Hooker's *Icones Plantarum, tt. 2819* and *2820*. In our opinion, these attributes render *C. wilsonii* synonymous with *C. multiflora*. *Corylopsis cavaleriei* was described in the absence of flowers (as was *C. cordata*); on the basis of leaf characters, the type of *C. cavaleriei* is placed in synonymy with *C. multiflora*. Neither the broader and more glabrous leaves of an isotype specimen of *C. cordata*, nor the shorter fruiting inflorescences and smaller fruits of the taxon, are thought to be sufficiently different from *C. multiflora* to warrant specific recognition. *Corylopsis cordata* is accordingly placed in the synonymy of *C. multiflora*. I (B. M.) have not examined specimens (*Tsang 24256* and *24747*) that are reputed to be labeled as *C. cordata*.

Known from Taiwan, plants recognized by Hayata as *Corylopsis stenopetala* are familiar to me (J. C.) (the type, collected by Ito in January, 1913, comes from Shinshikei). A flowering specimen, it has been likened

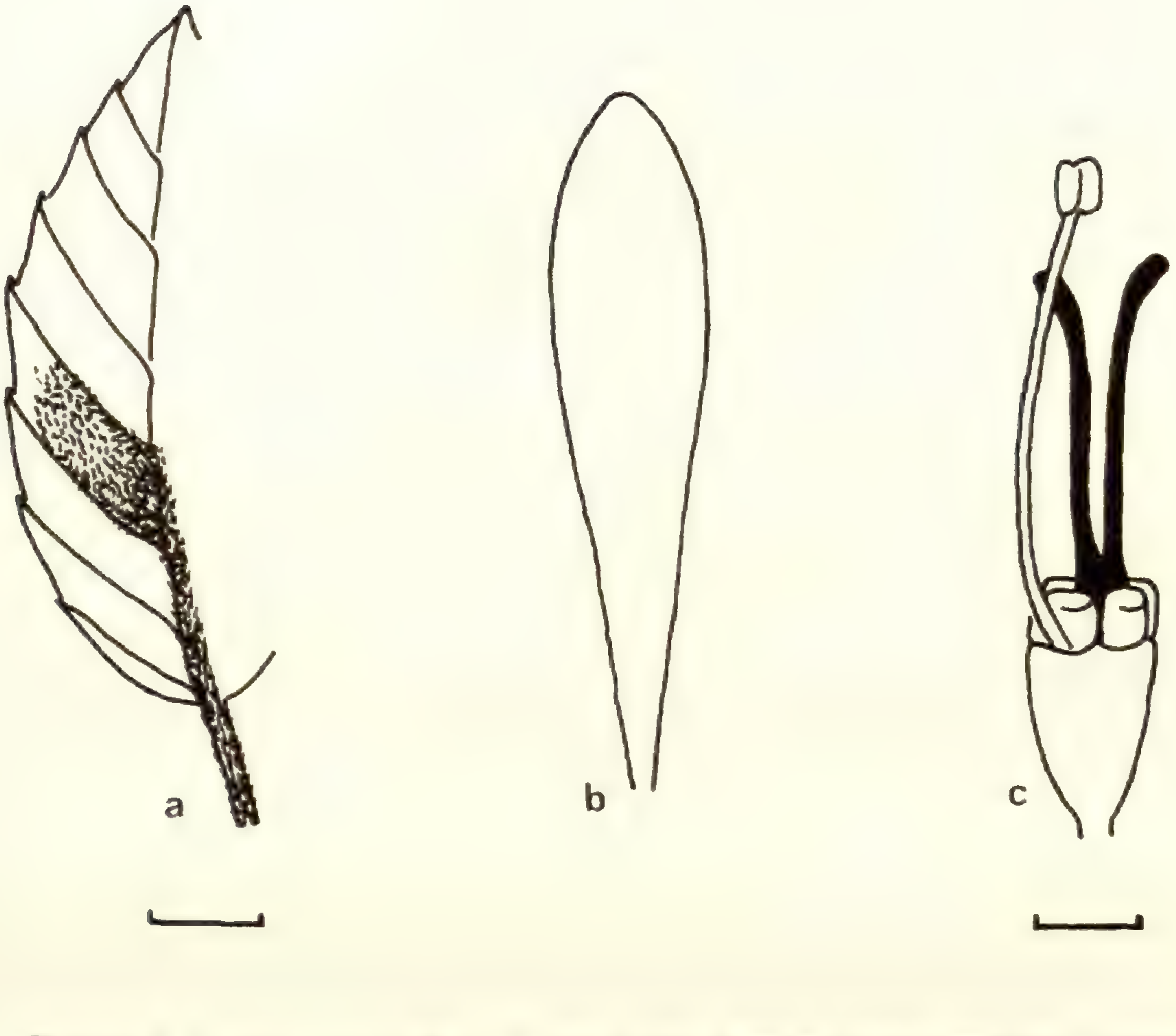


FIGURE 6. **Corylopsis multiflora:** a, leaf profile showing abaxial vestiture (*Hance 6684*, holotype); b, petal; c, flower with one stamen showing nectaries and styles (b, c after Smith in Hooker's Icon. Pl. **29:** *t. 2819*).

to *C. veitchiana*, but is clearly synonymous with *C. multiflora* and cannot be accepted as a distinct species.

The eighth edition of Bean (1970) takes over unchanged the entry for *Corylopsis* that appeared in the first edition of that work and lists *C. wilsonii* as cultivated in Britain. Both Rehder's *Manual* (1940) and Hillier's *Manual* (1974) include the species, but I (B. M.) have never seen material growing and doubt if *C. wilsonii* or *C. multiflora* are still in cultivation. As interpreted here, *C. multiflora* was introduced from Central China by E. H. Wilson for Messrs. Veitch in 1900 (see FIGURE 6).

4. **Corylopsis himalayana** Griffith, Jour. Asiatic Soc. Bengal **23**: 64. 1854; Hooker's Icon. Pl. **29**: *t. 2820*. 1906. HOLOTYPE: (*teste* Hemsley, 1906), *Griffith 593*, Tongsa, Bhutan (K).

4a. **Corylopsis himalayana** Griffith var. **himalayana.**

Corylopsis grata Griffith, Jour. Asiatic Soc. Bengal **23:** 64. 1854.
Corylopsis manipurensis Watt ex Hemsley, Hooker's Icon. Pl. **29:** *tt. 2819, 2820.* 1906. HOLOTYPE: *Watt 6434* (K!); isotype (E!).

Shrubs or small trees with pubescent or stellate-tomentose shoots; petioles glabrous, stellate-tomentose, or stipitate glandular, 3–4 cm. long; leaves ovate to ovate-lanceolate with acute apices and cordate to cuneate bases, the margins sinuate-denate, usually with bristle-like, excurrent teeth, 8–10 cm. long; abaxial surfaces of the leaf blades sericeous to brown tomentose or glabrous but pubescent-tomentose on the 8 to 12 pairs of veins; inflorescence 4–6 cm. long, 8–9 mm. in diameter, the rachis stellate-pubescent or tomentose; inflorescence bracts externally dark red-brown, glabrous; floral bracts externally glabrous to sericeous, usually pale brown-lanate; flowers 15 to 30, pale yellow, the sepals ca. 2 mm. long, ovate-elliptic, glabrous or pubescent; petals ca. 6 mm. long, obovate to elliptic, sometimes reduced to 1 in number; stamens and styles not seen fresh, nectaries 5, about as long as the sepals, bifid or deeply bifid, the stamens much shorter than the petals; ovary adnate to the pubescent hypanthium; capsules ± pilose, ca. 7–9 mm. in diameter.

LOCAL NAME. Pu-uir symrang. The flowers are cooked and eaten by local inhabitants in parts of the Himalayas (von Reis Altschul, 1973).

REPRESENTATIVE SPECIMENS. **India.** ASSAM: Bishops Falls, *Clarke 37381A* (BM); Shillong, *Ruse 3* (A); Chenna poory, *Gallatly 665* (BM); Chibaon Delei Valley, *Kingdon-Ward 8030* (K), *King s.n.* (K); Khasya, no further locality, *Hooker & Thomson s.n.* (E, K). MANIPUR: Sirohifurar, *Watt 6434* (E, K). **India-Burma:** Ngawchang Valley, *Kingdon-Ward 330* (A, BM); Sirhoi, *Kingdon-Ward 18261* (A, BM), *Kingdon-Ward 17205* (A, BM). **Bhutan:** Chukka-Chapcha Timpu, *Cooper 1316* (BM, E), *Griffith 3378* (K); Tongsa, *Cooper 2277* (BM, E); 26° N 92′ E, *Kingdon-Ward 6446* (K); Batte Dzong, *Ludlow et al. 16067* (BM, E); Satsa-lor-Diwangiri, *Ludlow et al. 1125* (BM, E), *Griffith s.n.* (K).

Corylopsis manipurensis was described in manuscript as a variety of *C. himalayana* by Sir George Watt, its discoverer, during the British Demarcation Survey of the eastern frontier of India in 1881–1882. As seen in *Watt 6434*, the reputed new taxon differed from *C. himalayana* by the occurrence of a single petal in each of the flowers. However, *C. himalayana* is now known to be polymorphic for petal length and number (e.g., *Ludlow et al. 1125* and *Kingdon-Ward 330*); the validity of *C. manipurensis* as a species is therefore doubted. The variability of the small elliptic leaves of *C. manipurensis* with an abaxial vestiture or glabrous lamina and pubescent veins, however, is not known. More collections and field observations are required. Plants corresponding to *C. manipurensis* are not commercially available and would probably be tender if grown in British gardens (see FIGURE 7, a–c, e, f).

Although Dr. King introduced seed of *Corylopsis himalayana* var. *himalayana* to Kew in 1879, and subsequent introductions were made by Messrs. Veitch, the variety was rare in cultivation (Goldring, 1889) and these stocks may now be lost in cultivation. Seed was sent to Glasnevin in 1972

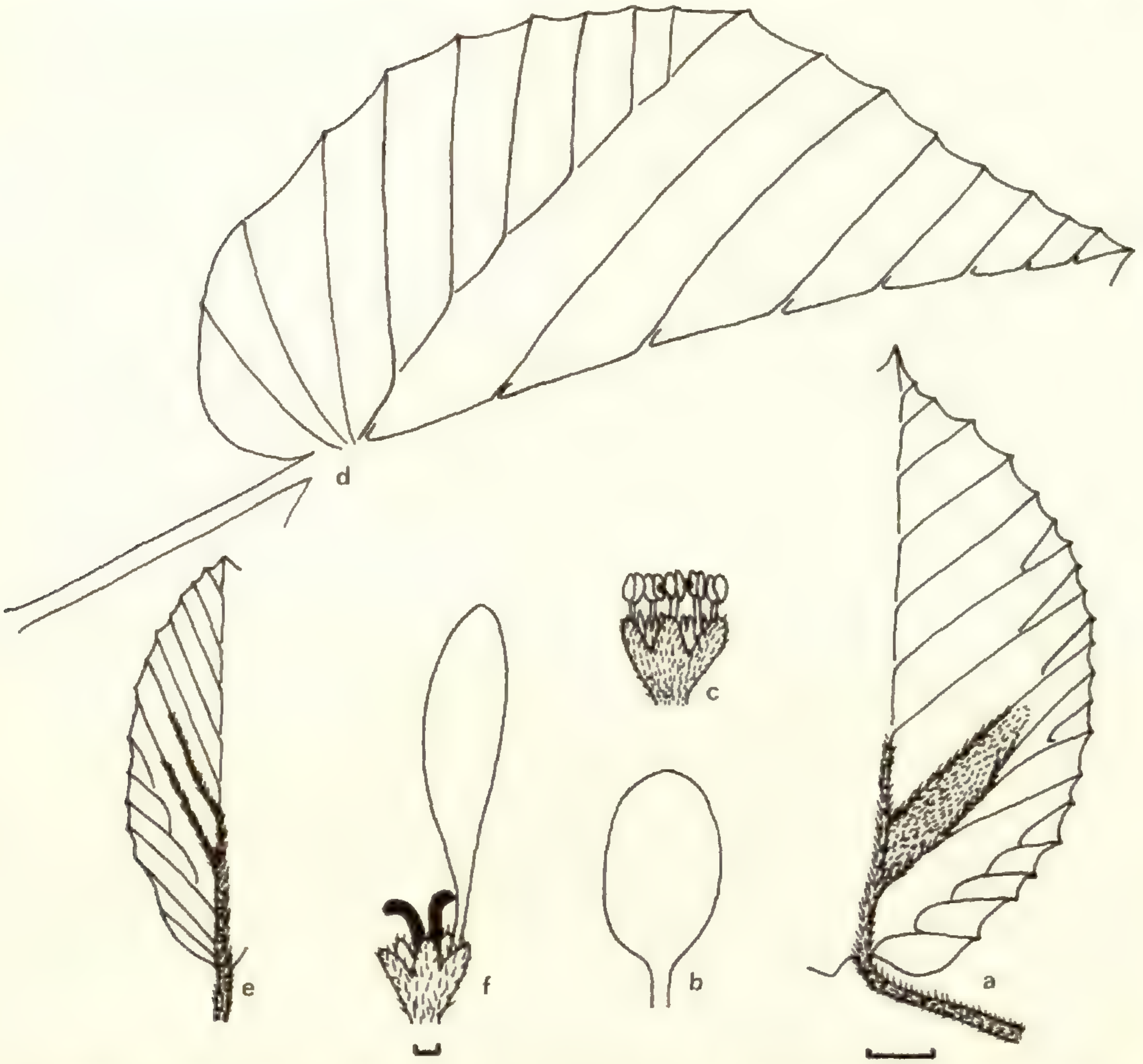


FIGURE 7. **Corylopsis himalayana.** a–c, e, f, *C. himalayana* var. *himalayana*: a, leaf profile showing abaxial vestiture (*Forrest 7802*); b, petal; c, flower without petals; e, leaf profile showing abaxial vestiture (*Kingdon-Ward 8030* as *C. manipurensis*); f, flower with only one petal (b, c, f after Smith in Hooker's Icon. Pl. **29:** *t. 2820*). d, *C. himalayana* var. *griffithii*: leaf profile (*Hooker & Thomson s.n.*).

by Dr. A. S. Rao of Shillong, and seedlings have been distributed to the major botanical gardens in the British Isles in an effort to re-establish the species in cultivation, if only in conservatories.

4b. Corylopsis himalayana Griffith var. **griffithii** (Hemsley) Morley & Chao, The Garden **102**(3): 106. 1977. BASIONYM: *Corylopsis griffithii* Hemsley, Gard. Chron. ser. 3. **39:** 19. 1906; Hooker, Curtis's Bot. Mag. **110:** *t. 6779*. 1884. HOLOTYPE: *Hooker & Thomson s.n.* (K!) (*teste* Hemsley, 1906, Bogu Panee, Khasya); isotype (BM!).

Plants that differ from *Corylopsis himalayana* var. *himalayana* in their larger leaves, the petioles to 6 cm. long and the blades to 20 cm. long with up to 17 pairs of veins, and by their larger inflorescences to 9 cm. in length and to ca. 13 mm. in diameter, are recognized here as *Corylopsis himalayana* var. *griffithii*.

William Griffith noted that *Corylopsis himalayana* was variable when he observed that differences existed between plants in Khasya and Bhutan. Recognition here of var. *griffithii* is based on size differences between the leaves and inflorescences of plants of *C. himalayana*. *Corylopsis himalayana* var. *griffithii* was introduced into cultivation in Europe by Dr. King, who sent seed to Kew in 1879, and later by Messrs. Veitch, who also introduced seed. Plants of var. *griffithii* are said to require the protection of a wall in Britain, but I (B. M.) know of no living specimens. It is not commercially available (see FIGURE 7, d).

REPRESENTATIVE SPECIMENS. **India.** ASSAM: Khasya, Mahlangwar, *Clarke 14675* (BM), *Hooker & Thomson s.n.* (BM, K); above Myrung, *Simons 112* (K), Herb. *Dresden s.n.* (A). **Burma-Tibet:** Adung Valley, *Kingdon-Ward 9281* (A, BM).

5. **Corylopsis spicata** Sieb. & Zucc., Fl. Japon. 1: 47. *t. 19*. 1835; Hooker, Curtis's Bot. Mag. 90: *t. 5458*. 1864. TYPES: *Siebold s.n.* (LE or L), not seen; *Siebold s.n.* (Herb. Zuccarini, 1843), Japan (K!).

Corylopsis kesakii Sieb. & Zucc., *op. cit.* 49.

Shrubs to ca. 3 m. with pubescent young shoots; petioles pubescent, 1–2.5 cm. long; leaves 4–11 cm. long, ovate to obovate with shortly acuminate apices, obliquely rounded to cordate bases, and sinuately dentate margins with bristle-like, excurrent teeth; abaxial surfaces of the leaf blades glaucous and densely pubescent, especially on the 6 to 8 pairs of veins; inflorescence 4–6 cm. long, ca. 1.2–1.5 cm. in diameter, the flowers clustered toward the distal end, the rachis pubescent, the inflorescence bracts glaucous, glabrous and reddish externally; floral bracts externally glabrous to sericeous at the margins; flowers 5 to 12, yellow, the sepals 3–4 mm. long, foliose, ovate-lanceolate, glabrous; petals 7–9 mm. long, obovate-spathulate; stamens with pink filaments, the anthers brown, purple, or red; nectaries 5, shorter than the sepals, bifid, with acute tips; ovary adnate to the pubescent brown hypanthium, the styles green; capsules pubescent, 7–8 mm. in diameter.

LOCAL NAME. Tosa-mizuki (Ohwi, 1965).

REPRESENTATIVE SPECIMENS. **Japan.** SHIKOKU: Nishikiyama Hill, Pref. Kochi, *Murata 17913* (E, K); Nangoku-shi, *Ohashi s.n.* (A), *Faurie 11919* (K). HONSHU: Central Mountains, *Maries s.n.* (K), *Wilson 6323* (BM); Yokohama, *Bisset s.n.* (BM); Yokohama hort., *Bisset 1722* (E), Herb. *Drake s.n.* (K); Mino Prov. *Shiota 8318* (A), *Shiota 7430* (flowers) & *3325* (leaves) (A); Kobe, *Muroi 270* (A). KYUSHU: Nagasaki hort., *Maximowicz 9995* (BM); Nagasaki, *Maximowicz s.n.* (GH, K), *Wilson 6230* (K); Rokugawa hort., *Bisset 1723* (BM, K). JAPAN, without further locality, *Siebold s.n.* (Herb. Zuccarini, 1843, K).

According to Bretschneider (1898), Robert Fortune introduced *Corylopsis spicata* to England in 1860 or 1861, and Messrs. Veitch made commercial introductions from Yokohama in 1863. *Corylopsis spicata* is one of the first corylopses to flower each spring in western Europe, which is compensation for its rather untidy inflorescences, characteristically brac-

teate but flowerless in the upper part with flowers concentrated at the free end of the rachis. The petals are spathulate and the sepals somewhat leafy, characters which distinguish the species from the continental *C. sinensis*, which also has pubescent undersides to the leaves. *Corylopsis spicata* is widespread in cultivation at present and is still commercially available (see FIGURE 8).

6. **Corylopsis glabrescens** Franchet & Savatier, Enum. Pl. Jap. **2:** 367. 1878. HOLOTYPE: *Rein s.n.* (P), Satzuma Prov., Japan, not seen.

Corylopsis gotoana Makino, Bot. Mag. Tokyo **15:** 111. 1901. SYNTYPE: *Goto s.n.* (MAK or TI?), Kiso, Shinano Prov., Japan, not seen.

Corylopsis coreana Uyeki, Suigen Gakuho. No. **41.** 1924; Jour. Chosen Nat. Hist. Soc. **20:** 15. 1935.

Shrubs to ca. 6 m., the young shoots glabrous; petioles 1.5–3 cm. long, sparsely sericeous, in age often glabrous; leaves 3–8 cm. long, ovate to suborbicular with acuminate apices, obliquely cordate to subcordate bases, and sinuate-dentate margins with excurrent, bristle-like teeth; abaxial surfaces of the leaf blades glaucescent, sparsely sericeous on the 7 to 12 pairs of veins; inflorescences 2–5 cm. long, ca. 8 mm. in diameter, the rachis glabrous; inflorescence bracts glabrous, glaucous, and reddish externally;

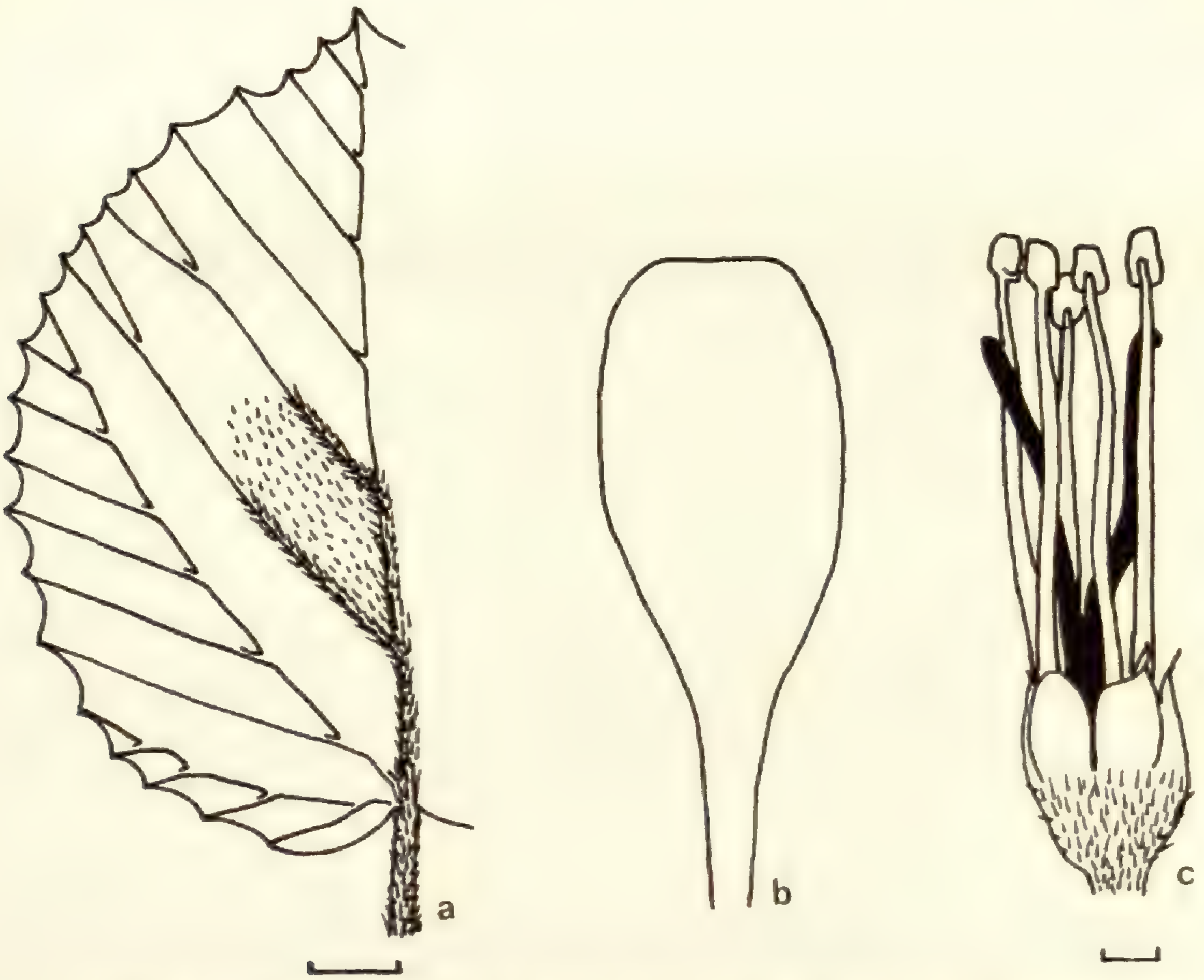


FIGURE 8. **Corylopsis spicata:** a, leaf profile showing abaxial vestiture (*Bisset 1723*); b, petal; c, flower without petals (flowers cultivated in Glasnevin as *C. spicata*).

floral bracts glabrous to sparsely sericeous; flowers 10 to 22, yellow, widely but evenly spaced along the rachis; sepals ca. 1 mm. long, obtusely triangular, fleshy and glabrous; petals to 8 mm. long, orbicular to obovate; stamens with yellow filaments, the anthers yellow or purple, the 5 nectaries longer than the sepals, bifid with obtuse tips, greenish, sometimes purplish; ovary adnate to the glabrous hypanthium, the styles green; capsules glabrous, 6–8 mm. in diameter.

LOCAL NAMES. Kirishima-mizuki, Kōya-mizuki, Miyama-Tosa-mizuki, (Ohwi, 1965).

REPRESENTATIVE SPECIMENS. **Japan.** KYUSHU: Mt. Kirishima, *Tashiro s.n.* (K), *Wilson 6230* (A); Mt. Kirishima, *Naito 123* (A); Satzuma Prov., *Rein s.n.* (P), not seen. HONSHU: near Otake, *Wilson 7763* (A, K), *Wilson 7032* (A, K); Mt. Aterayama, *Murata & Iwatsuki 908* (E, K). **Korea:** Sinto Village, Okayama Pref., *Muroi 1032* (A).

Corylopsis gotoana, here placed in the synonymy of *C. glabrescens*, commemorates Suekichi Goto, a former assistant in the Dendrology Institute of the Imperial University of Tokyo. Goto collected a syntype of *C. gotoana* and Makino described the taxon in the absence of flowers. Plants of *C. gotoana* are stated by Ohwi (1965) to differ from those of *C. glabrescens* in the length of the stamens and in the margins of the leaves, but these differences are not considered here to warrant specific recognition. Moreover, the type description of *C. coreana* closely resembles that of *C. glabrescens*, and *C. coreana* is tentatively made synonymous. According to Li (1962), Professor J. G. Jack first introduced *C. glabrescens* into North America in 1905. It was subsequently introduced to Kew in 1916 and is still commercially available, being widely cultivated under a variety of names, including *C. gotoana* and *C. platypetala* (see FIGURE 9).

7. **Corylopsis sinensis** Hemsley, Gard. Chron. ser. 3. **39**: 18. 1906. HOLOTYPE: *Wilson 691* (K!).

7a. **Corylopsis sinensis** Hemsley var. **sinensis.**

Corylopsis glandulifera Hemsley, *op. cit.* 18. 1906. HOLOTYPE: *Maries s.n.* (K!).

Corylopsis yunnanensis Diels, Notes Bot. Gard. Edinburgh **5**: 226. 1912. HOLOTYPE: *Forrest 4095* (E!); isotypes (GH!, K!).

Corylopsis sinensis Hemsley var. *glandulifera* (Hemsley) Rehder & Wilson, Pl. Wilsonianae **1**: 424. 1913.

Corylopsis willmottiae Rehder & Wilson, Pl. Wilsonianae **1**: 425. 1913. HOLOTYPE: *Wilson 1316* (AAH!); isotypes (E!, K!).

Corylopsis velutina Hand.-Mazz., Anz. Akad. Wiss. Wien Math. Nat. **62**: 130. 1925. ISOTYPE: *Handel-Mazzetti 1810* (E!).

Corylopsis willmottiae Rehder & Wilson var. *chekiangensis* Cheng, Contr. Biol. Lab. Sci. Soc. China **10**: 125. 1936. HOLOTYPE: *Chen 2772* (PE?), Yunho. Chekiang, not seen.

Corylopsis polyneura Li, Jour. Arnold Arb. **25**: 299. 1944. HOLOTYPE: *Wang 66783* (PE!), photograph seen.

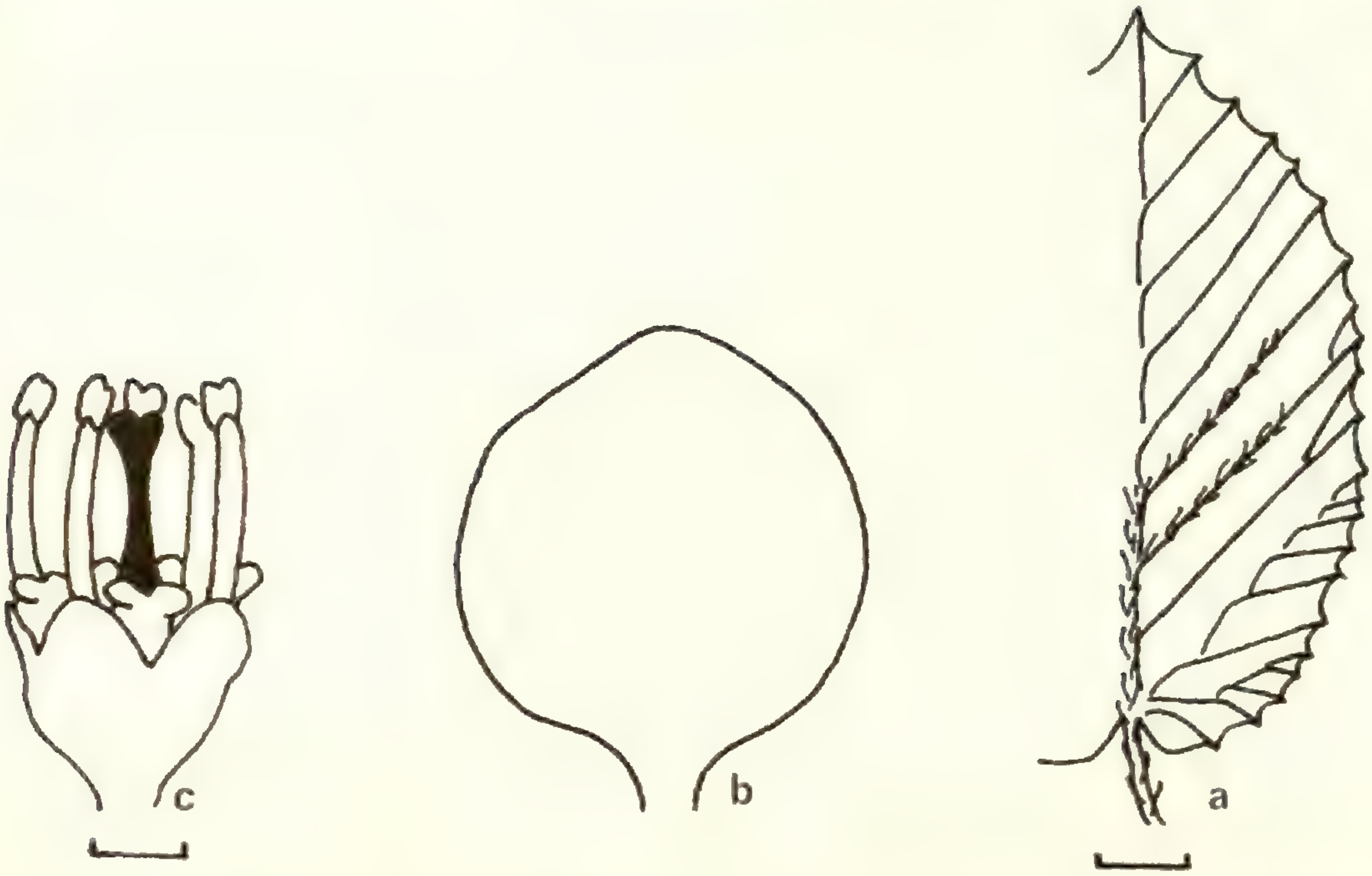


FIGURE 9. **Corylopsis glabrescens:** a, leaf profile showing abaxial vestiture (*Tashiro s.n.*); b, petal; c, flower without petals (flowers cultivated in Glasnevin as *C. gotoana*).

Corylopsis obovata H. T. Chang, Sunyatsenia **7**: 72. *t.* 13. 1948. HOLOTYPE: *Ho 51313* (PE?), Yinkiang, Fanching Shan, not seen.

Corylopsis trabeculosa Hu & Cheng, Bull. Fan Mem. Inst. Biol. Peiping **1**: 192. 1948. HOLOTYPE: *Yu 21059* (PE!), photograph seen; isotypes (A!, E!).

Corylopsis yui Hu & Cheng, Bull. Fan Mem. Inst. Biol. Peiping **1**: 193. 1948. HOLOTYPE: *Yu 19509* (PE!), photograph seen; isotypes (A!, E!).

Shrubs to 5 m. with glabrous or villose (and then, eventually glabrous) young shoots; petioles 5–15 mm. long, glabrous and glaucous or usually sericeous-pubescent, rarely glandular; leaves 5–12 cm. long, obovate to oblong-elliptic, with acuminate apices, obliquely cordate to subcordate or rounded bases, and sinuately dentate margins with bristle-like, excurrent teeth; abaxial surfaces of the leaf blades sericeous to densely brown-pubescent, rarely pubescent only on the 7 to 12 pairs of veins or brown-tomentose throughout, the lamina often with secondary reticulate veins; inflorescence 2–9 cm. long, ca. 1 cm. in diameter, with the rachis sericeous to densely pubescent; inflorescence bracts externally glabrous and glaucous to sparsely pubescent and dark brown; floral bracts externally pubescent to sericeous, rarely glabrous; flowers 6 to 35, yellow, evenly and densely spaced along the rachis; sepals fleshy, 0.5–1.5 mm. long, obtusely triangular to ovate, glabrous, pilose, or ciliate at the margin; petals 7–8 mm. long, orbicular to suborbicular; stamens with greenish filaments, the anthers yellow; nectaries 5, longer than the sepals, bifid, sometimes deeply so, the tips acute; ovary adnate to the pubescent or glabrous hypanthium, the styles greenish; capsules pubescent to subtomentose, rarely glabrous, 6–9 mm. in diameter.

REPRESENTATIVE SPECIMENS. **China.** KIANGSI: Kuling, *Wilson 1556* (BM, E); Lu Shan, *Chung & Sun 182* (A); Kiukiang, *Maries s.n.* (K), *Carles s.n.* (E), *Faber 929* (K); Lu Shan, *Steward 2473* (A, E, K). HUPEH: Changyang, *Wilson 691* (K), *Wilson 65* (A, K); Chienshih, *Henry 5854* (K). HUNAN: Hsinhwa, *Handel-Mazzetti 11771* (E, K). SZECHUAN: Tachienlu, *Wilson 1316* (AAH, E, K), *Wilson 4406* (K); Mupin, *Wilson 4224* (K); Techang, *Schneider 753* (K); Sungpan hsien, *Fang 4180* (E, K); Hanyuan hsien, *Fang 3750* (E, K). WESTERN SZECHUAN-TIBET: *Pratt 85* (E, GH, K). CHEKIANG: Tienmushan, *Liou 255* (K). ANHWEI: Wangsi che, *Ching 2849* (E, K); Wang shan, *Ching 3064* (K); Chu Hwa Shan, *Ching 2598* (K), *Chang 1694* (K). YUNNAN: Doker-la, *Forrest 17174* (E, K); Tengyueh-Likiangfu, *Rock 8127* (A); Tali, *McClaren C26* (A), *Delavay 4729* (K), *Forrest 13516* (E, K), *Schneider 2794* (A, K); Mt. Isang, Tali, *Delavay 256* (E, K); Tali Range, *Forrest 7252* (E, K); Lan-Ping hsien, *Tsai 54031* (A); Tai-pou, *Maire 92* (K); Lao-keou, *Maire 519* (K); Tchou-nen-tseu, *Maire 537* (K); Che-kia-po, *Maire 104* (A, K); west Talifu, *Forrest 4095* (E, GH, K); Taron Valley, *Yu 20180* (E), *Yu 21059* (E, GH), *Yu 19509* (A, E); Ming kwong Valley, *Forrest 7802* (E). SOUTHWEST CHINA–EASTERN TIBET: Chienchuan-Mekong Divide, *Forrest 23588* (K).

The occurrence of glandular hairs on occasional plants does not, in our opinion, merit taxonomic recognition. As a result, the names *Corylopsis glandulifera* and *C. sinensis* var. *glandulifera* are placed in the synonymy of *C. sinensis* var. *sinensis*. Likewise, *C. yunnanensis* is placed in synonymy since the characters used to distinguish plants of this taxon (shorter styles, number and shape of nectaries, and foliage characters) fall within the range of variation encountered for those characters in *C. sinensis*.

Other plants (well known in gardens under the name *Corylopsis willmottiae*) are difficult to distinguish from *C. sinensis* except for their yellow anthers, long inflorescences, and variously pubescent lower leaf surfaces. Herbarium specimens of plants referred to *C. willmottiae* frequently possess a reticulation of the underside of the lamina caused by secondary veins, but this reticulation is by no means a constant character. It would be difficult to maintain plants now passing under the name *C. willmottiae* even as a cultivar due to the lack of constant characters to distinguish the plants from other variants of *C. sinensis*. As a result, we have placed the name *C. willmottiae* in synonymy.

Plants grown under the name *Corylopsis willmottiae* were first introduced by E. H. Wilson in 1909 from western Szechuan, and an Award of Merit was given to the species (exhibited as *C. multiflora*, with which it was confused) by the Royal Horticultural Society in 1912. The garden value of these plants is perhaps due, in part, to the fact that they are tetraploids, not diploids like the majority of plants of *C. sinensis* (see FIGURE 10, d, e).

Although plants segregated as *Corylopsis velutina* are in some ways intermediate between plants of *C. sinensis* and *C. himalayana*, *C. velutina* is placed in the synonymy of *C. sinensis*. This decision has been made after studying the type of *C. velutina*, collected within the range of *C. sinensis* near Dotschang in the province of Szechuan (*Handel-Mazzetti 1810*), and considering the variation encountered in *C. sinensis*.

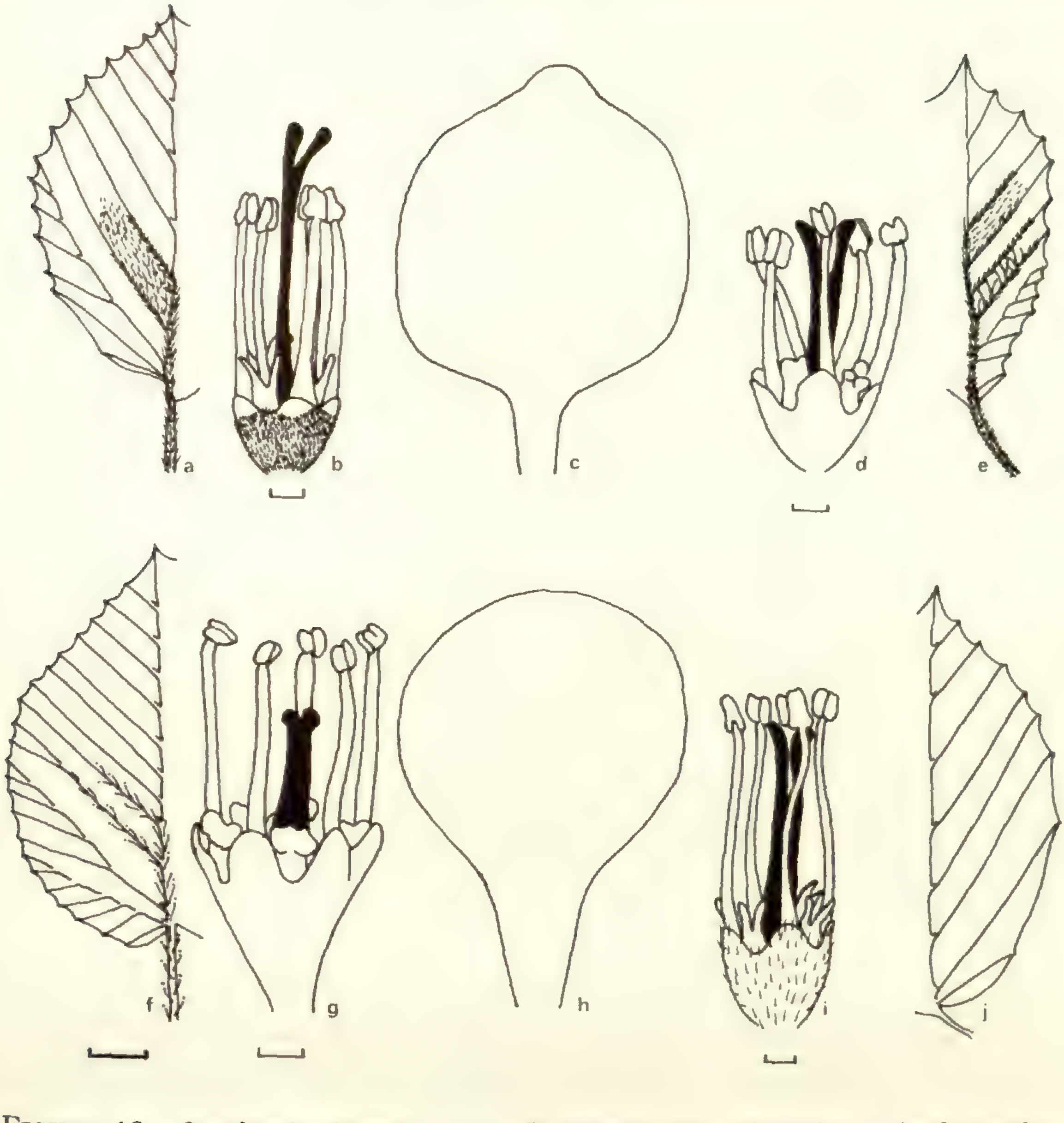


FIGURE 10. **Corylopsis sinensis.** a–e, *C. sinensis* var. *sinensis*: a, leaf profile showing abaxial vestiture (*Law 1205*); b, flower without petals; c, petal (flowers cultivated in Glasnevin as *C. sinensis*); d, flower without petals (cultivated in Glasnevin as *C. willmottiae*); e, leaf profile showing abaxial vestiture and secondary vein reticulations (*Wilson 1316*, holotype of *C. willmottiae*). f–j, *C. sinensis* var. *calvescens*: f, leaf profile showing abaxial glandular vestiture (*Wilson 184*, holotype of *C. platypetala*); g, flower without petals; h, petal (flowers cultivated in Glasnevin as *C. platypetala*); i, flower without petals (cultivated in Glasnevin as *C. veitchiana*); j, leaf profile showing lack of vestiture (*Veitch s.n.*, holotype of *C. veitchiana*).

Only photographs of the *Corylopsis polyneura* holotype have been available to us, but, in conjunction with the type description, it is evident that plants of this taxon relate to *C. sinensis*. The type specimen, *Wang 66783* (not *Wang 66738* as sometimes quoted), was collected from Cham-putong, Yunnan Province, in October, 1935, and is, consequently, of a fruiting plant. Similarly, the type of *C. obovata*, *Ho 51313*, from Yinkiang, Fanching Shan, is also in fruit, having been collected in July of 1931. Although we have not seen the type specimen, the protologue states that the fruits and the abaxial surfaces of the leaves of *C. obovata* are pubes-

cent. These features suggest strongly that the name *C. obovata* is synonymous with *C. sinensis*.

Plants described as *Corylopsis trabeculosa* are intermediate in some features between plants of *C. sinensis* and *C. himalayana*. The holotype of *C. trabeculosa*, *Yu 21059* (not *Yu 21505* as stated by Hu & Cheng, 1948), was collected from Tsunwangtu, in the Taron Valley, on 21 November, 1938 (PLATE I). Another specimen, *Yu 20180* (not *Yu 29480* as stated by Hu & Cheng, 1948), was also collected in the Taron (Kiukiang) Valley, Chunwangtum, Yunnan, and is a fruiting specimen that was collected on 7 September, 1938. The abaxial surfaces of the leaves of these specimens are stated to be densely brown-tomentose, rather like some specimens of *C. himalayana*, and the tomentose infructescence contains 30 or more fruits (PLATE I).

The last species name placed in synonymy of *Corylopsis sinensis* var. *sinensis*, *C. yui*, was based on specimens collected by T. T. Yu (no. *19509*), a collection comprising fruiting material and, like plants of *C. trabeculosa*, also collected in the Taron Valley at Ching-tinglaka Shan. We have seen *Yu 19509* at the Edinburgh Botanic Garden and have received photographs of the holotype housed in the Botanical Institute of the Academia Sinica, Peking. We have also studied a paratype, *Yu 20223*, from the Salwin-Taron Divide west of Wangtzang, which is a specimen with flowers. The pubescent abaxial surfaces of the leaves and the glabrous fruits refer the specimens to *C. sinensis*, and the name *C. yui* is placed in synonymy (see FIGURE 10, a–c). *Forrest 7802* from the "flanks of the Ming kwong Valley," Yunnan, is also intermediate between *C. sinensis* and *C. himalayana* and requires more detailed study. Additional material is needed to arrive at definite conclusions concerning these plants and their relationships since the variation seen in *C. sinensis* var. *sinensis* is not only chromosomal, but may also involve hybridization.

7b. Corylopsis sinensis Hemsley var. **calvescens** Rehder & Wilson, Pl. Wilsonianae **1**: 424. 1913. HOLOTYPE: *Wilson 1554* (A!); isotypes (BM!, E!).

C. veitchiana Bean, Curtis's Bot. Mag. **136**: *t. 8349*. 1910. HOLOTYPE: *Veitch 1909* (K!).

Berchemia alnifolia Léveillé, Feddes Repert. **10**: 433. 1912. ISOTYPES: *J. Cavalerie 2712* (E!, K!).

C. alnifolia (Léveillé) Schneider, Feddes Repert. **12**: 379. 1913.

C. platypetala Rehder & Wilson, Pl. Wilsonianae **1**: 426. 1913. HOLOTYPE: *E. H. Wilson 184* (GH!); isotypes (A!, E!, K!).

C. platypetala Rehder & Wilson var. *levis* Rehder & Wilson, *Ibid.* **1**: 427. 1913. HOLOTYPE: *E. H. Wilson 1020* (GH!); isotype (BM!).

C. glaucescens Handel-Mazzetti, Anz. Akad. Wiss. Wien Math. Nat. **62**: 130. 1925. ISOTYPES: *Handel-Mazzetti 9018* (E!, GH!, K!).

C. hypoglauca Cheng, Contr. Biol. Lab. Sci. Soc. China Bot. Ser. **10**: 169. 1936. HOLOTYPE: *Pei 3870* (PE?), Wangshan, Anhwei, not seen.

C. hypoglauca Cheng var. *glaucescens* Cheng, Contr. Biol. Lab. Sci. Soc. China

Bot. Ser. **10:** 126. 1936. HOLOTYPE: *Chen 430* (PE?), Tientaishan, Chekiang, not seen.

C. omiensis Yang, *Ibid.* **12:** 133, 136. 1941. HOLOTYPE: *Wu 10941* (PE?), Omei-shan, Szechuan, not seen.

Shrubs to 4 m.; shoots glabrescent or glabrous, sometimes stipitate-glandular when young; petioles 5–25 mm. long, sparsely stipitate-glandular, sericeous, or glabrous; leaves 5–10 cm. long, ovate to elliptic, with shortly acuminate or rarely retuse apices, cordate to subcordate bases, and sinuately dentate margins with bristle-like, excurrent teeth; abaxial surfaces of the leaf blades glaucescent and sparsely sericeous on the 6 to 11 pairs of veins, or sometimes glaucous and glabrous, the lamina between the primary veins smooth when dry; inflorescences 2.5–5 cm. long, ca. 1 cm. wide, the rachis sericeous or glabrous and glaucous; inflorescence bracts dark brown and glabrous on the abaxial surfaces; floral bracts externally glabrous to sericeous at the margins; flowers 9 to 30, yellow, closely and evenly spaced along the rachis; sepals fleshy, to 2 mm. long, obtusely triangular to ovate, glabrous or sparsely pubescent or rarely ciliate at margin, sometimes glaucous; petals 4–6 mm. long, orbicular to reniform in outline; stamens with yellowish or green filaments, the anthers yellow or red; nectaries 5, longer than the sepals, green or purplish, bifid, sometimes deeply so, the tips acute or obtuse; ovary adnate to the glabrous or pilose hypanthium, the style yellowish or green; capsules glabrous to sparsely pilose, 4–10 mm. in diameter.

REPRESENTATIVE SPECIMENS. **China.** KIANGSI: Kuling, *Wilson 1554* (A, BM, E). HUPEH: Hsing-shan hsien, *Wilson 184* (A, E, GH, K); Changyang hsien, *Wilson 173A* (BM, E, K), *Wilson 65 = 448* (E, K, a mixture of *C. platypetala* and *C. sinensis* var. *sinensis*), *Wilson 173* (A, E, GH, K), *Wilson 449* (K). SZECHUAN: near Mt. Omei, *Chow 11749* (A), *Chow 11418* (A); Tien-chuan hsien, *Chu 2617* (E); Wen ch'uan hsien, *Wilson 1020* (BM, GH); Mupin, *Wilson 2274* (BM); Ching-chi hsien, *Wilson 2273* (E, K); Mao-chou, *Wilson 2272* (E, K); Mo-tsou (= Mao-chou?), *Maire 1241* (E); Omei hsien, *Chien 5581* (E). CHEKIANG: Ping Shan hsien, *Wang 22779* (A); Chen Chiong, *Ching 1767* (E); Tien-tai Shan, *Keng 1062* (A); Tihtaishan, *Ching 1422* (E, K); King yuan, *Ching 2356* (E, K), *Faber 177* (K). ANHWEI: Wang Shan, *Chow 121* (A), *Ching 2965* (E, K), *Ching 2728* (K). KWEICHOW: Fan Ching Shan, *Steward et al. 571* (K); Ma Jo, *Cavalerie 3185* (E), *Cavalerie 7146* (K); Kwei Yang, *Cavalerie 2712* (E, K). YUNNAN: north east of Atuntze, *Forrest 19857* (A); near Bahan (Pehalo), Salween River, *Handel-Mazzetti 9018* (E, GH, K). **Tibet.** EASTERN TIBET: Tsarong, Salwin-Kiu Chiang Divide, *Forrest 20853* (E). SOUTHEAST TIBET: Mt. Kenyichunpo, *Rock 11226* (A), *Rock 10177* (A).

Horticulturists are familiar with plants of *Corylopsis veitchiana*, which have red, exserted stamens and abaxially glabrous leaves. It is not possible to maintain this species, however, when the variation of others is considered. For the purposes of convenience to horticulture it is possible to recognize plants of *C. veitchiana* as a form of *C. sinensis* var. *calvescens*, as follows:

7a$_1$. **Corylopsis sinensis** Hemsley var. **calvescens** Rehder & Wilson forma **veitchiana** (Bean) Morley & Chao, The Garden 102(3): 107. 1977. BASIONYM: *Corylopsis veitchiana* Bean, Curtis's Bot. Mag. **136**: *t. 8349*. 1910.

The forma *veitchiana* is recognized by its red anthers and abaxially glabrous leaves, which distinguish it from the other garden plants of *Corylopsis* with red anthers, viz. *C. spicata*. Introduced to Kew by Wilson in 1900 from Changyang in Hupeh Province of China, forma *veitchiana* was later (1908) introduced to North America by the Arnold Arboretum from the same locality. The Changyang area was first explored by Augustine Henry and was worked over by one of his collectors about 1887 (Morley, in press). Unlike garden plants called *C. platypetala* (another name here made synonymous with *C. sinensis* var. *calvescens*), forma *veitchiana* is not diploid but hexaploid and is still available commercially (see FIGURE 10, i, j).

Schneider recognized that *Berchemia alnifolia* of Léveillé was in fact a *Corylopsis*, and he made the necessary transfer in 1913. From an examination of type material of *C. alnifolia*, it is evident that the plant is no more than var. *calvescens*. No useful distinction can be found between either variety of *C. platypetala* and *C. sinensis* var. *calvescens* since all have glabrescent leaves, more or less glabrous hypanthia, and orbicular petals. According to Rehder and Wilson (1913), the differences between *C. platypetala* and its variety *levis* break down because seedling leaves of var. *levis* have the glandular hairs that characterize var. *platypetala*. Furthermore, var. *levis* was described from vegetative material only. We consider both varieties of *C. platypetala* synonymous with var. *calvescens*. Plants passing under the name *C. platypetala* are still in commerce, the var. *platypetala* having been introduced by Wilson from Hupeh in 1907, and the var. *levis* a year later.

Corylopsis glaucescens has never been available commercially, although some forms of *C. glabrescens* from Japan approach the glaucous condition that characterizes the former species. Because we do not think that *C. hypoglauca* or *C. hypoglauca* var. *glaucescens* Cheng can be usefully distinguished from *C. glaucescens*, we make both synonymous with *C. sinensis* var. *calvescens* on the basis of examined type material of *C. glaucescens* and diagnoses. *Corylopsis omiensis* closely approximates var. *calvescens* on the basis of the type description and is, therefore, made synonymous (see FIGURE 10, f–h).

CONCLUSIONS

It has been necessary to reduce many of the described binomials of *Corylopsis* to synonymy in order to begin to make some sort of sense out of the genus. We are aware that this study is only a beginning, but hope that this reassessment may help to stimulate more synthetic research on the group. Except for scattered contributions by workers such as Tong (1930) and Jay (1968), there has been little attention given to *Corylopsis*

apart from the formal and, it seems, sometimes uncritical description of new taxa. The cytology, floral biology, and horticultural value of the group all warrant a more detailed approach both in the field and under cultivation.

Three projects requiring field work suggest themselves from our herbarium- and botanic garden-based studies: (a) a detailed assessment of the systematic relationship between *Corylopsis himalayana* and *C. sinensis* var. *sinensis*, (b) assessment of the variation seen in *C. sinensis* sensu lato, and (c) assessment of the systematic relationship between *C. sinensis* var. *calvescens* and *C. glabrescens*.

ACKNOWLEDGMENTS

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MORLEY & CHAO, CORYLOPSIS

Corylopsis sinensis var. *sinensis* (*Yu 21059*, holotype of *C. trabeculosa*).

A REVISION OF THE GENUS BOSISTOA (RUTACEAE)*

THOMAS G. HARTLEY

THE RAIN FORESTS of eastern Australia harbor a number of endemic, apparently relict genera of the Rutaceae. One such genus is *Bosistoa* F. Mueller ex Bentham, which consists of seven species of understory or subcanopy trees and ranges from the Cape York Peninsula south to northeast New South Wales (see MAPS 1–3).

Bentham described *Bosistoa* in 1863, basing it on *Euodia pentacocca* F. Mueller. In this original description the illegitimate name *Bosistoa sapindiformis* F. Mueller ex Bentham was used for the type species. This plant is now correctly known as *B. pentacocca* (F. Mueller) Baillon. Since 1863, three other species have been described in the genus, *B. euodiiformis* F. Mueller, *B. connaricarpa* Domin, and *B. transversa* Bailey & White. *Bosistoa euodiiformis* has proven to be out of place in this assemblage, and I have recently (Jour. Arnold Arb. **58**: 176. 1977) transferred it to *Acradenia* (Rutaceae).

The genus *Pagetia* F. Mueller, in which three species (*P. medicinalis* F. Mueller, *P. monostylis* F. M. Bailey, and *P. dietrichiae* Domin) have been described, is considered here to be taxonomically synonymous with *Bosistoa*. Although there are considerable differences in leaf characteristics between the type species of the two genera, *Bosistoa pentacocca* and *Pagetia medicinalis* (the former having pinnately compound, crenately or serrately margined leaves, and the latter having predominantly unifoliolate, entire leaves), there are no fundamental differences in reproductive characters, and there are significant bud similarities. Also, when a range of material of the other taxa of *Bosistoa* and *Pagetia* is examined, it becomes evident that the significance of the leaf differences between the two type species breaks down.

Bosistoa is distinguishable from all of the known genera of the Rutaceae in the Indo-Pacific region in having the following combination of characters: opposite leaves, 5-merous flowers, multi-ovulate carpels, and follicular fruits.

The Australian rain forest genus *Bouchardatia* Baillon (not including *Bouchardatia cyanosperma* Ridley, described from New Guinea) appears to be the closest relative of *Bosistoa*. The main differences and similarities between these two genera are given below.

Bosistoa	*Bouchardatia*
Leaves opposite	Leaves opposite
Leaves without domatia	Leaves with domatia
Leaf and floral primordia enclosed by bud scales	Leaf and floral primordia not enclosed by bud scales
Inflorescences terminal or terminal and upper axillary	Inflorescences terminal or terminal and upper axillary

* This is the tenth in a series of papers on the Rutaceae of Malesia and Australasia.

Sepals, petals, and carpels 5	Sepals, petals, and carpels 4
Stamens 10	Stamens 8
Ovules 4–6 per carpel	Ovules 6–8 per carpel [1]
Testa pergamentaceous	Testa pergamentaceous
Endosperm absent	Endosperm scant

This study is based on herbarium specimens. The contributing herbaria are as follows, with abbreviations, where available, from Holmgren and Keuken's *Index Herbariorum*, Part 1. ed. 6 (Reg. Veg. 92. 1974); Arnold Arboretum of Harvard University, Cambridge (A); Bernice P. Bishop Museum, Honolulu (BISH); British Museum (Natural History), London (BM); Queensland Herbarium, Brisbane (BRI); Botanical Survey of India, Calcutta (CAL); C.S.I.R.O. Herbarium Australiense, Canberra (CANB); New South Wales Forestry Commission, Coffs Harbour (COFFS HARBOUR); Gray Herbarium of Harvard University, Cambridge (GH); Allgemeine Botanik, Hamburg (HBG); Royal Botanic Gardens, Kew (K); Rijksherbarium, Leiden (L); National Herbarium of Victoria, Melbourne (MEL); National Herbarium of New South Wales, Sydney (NSW); New York Botanical Garden, New York (NY); Muséum National d'Histoire Naturelle, Paris (P); Botanical Department, National Museum, Prague (PR); C.S.I.R.O. Queensland Research Station, Atherton (QRS); Botanical Museum and Herbarium, Utrecht (U); Herbarium of the University of California, Berkeley (UC); National Museum of Natural History (Department of Botany), Smithsonian Institution, Washington, D.C. (US); and Naturhistorisches Museum, Wien (W).

Bosistoa F. Mueller ex Bentham, Fl. Austral. 1: 359. 1863. TYPE SPECIES: *Euodia pentacocca* F. Mueller [*Bosistoa pentacocca* (F. Mueller) Baillon].

Pagetia F. Mueller, Frag. Phytogr. Austral. 5: 178. 1866. TYPE SPECIES: *Pagetia medicinalis* F. Mueller.

Small to medium trees; indumentum of simple trichomes; buds with scales completely enclosing the leaf and floral primordia. Leaves opposite, imparipinnate, pinnately trifoliolate, or unifoliolate, pinnately veined, with pellucid oil dots. Inflorescences paniculate, many-flowered, terminal or terminal and from the axils of the upper leaves. Flowers bisexual, globose in bud; sepals 5, pellucid-dotted, connate or distinct, basally imbricate or valvate, persistent or deciduous in fruit; petals 5, white, pellucid-dotted, distinct, valvate, hoodlike and somewhat hooked adaxially at the apex, becoming reflexed, deciduous in fruit; stamens 10, at anthesis the antesepalous about as long as the petals and the antepetalous slightly shorter, filaments glabrous, straight, linear to narrowly lanceolate, tapering to a subulate apex, anthers 2-celled, versatile, dehiscing by longitudinal slits, elliptic; disc intrastaminal, pulvinate to columnar, angled or slight-

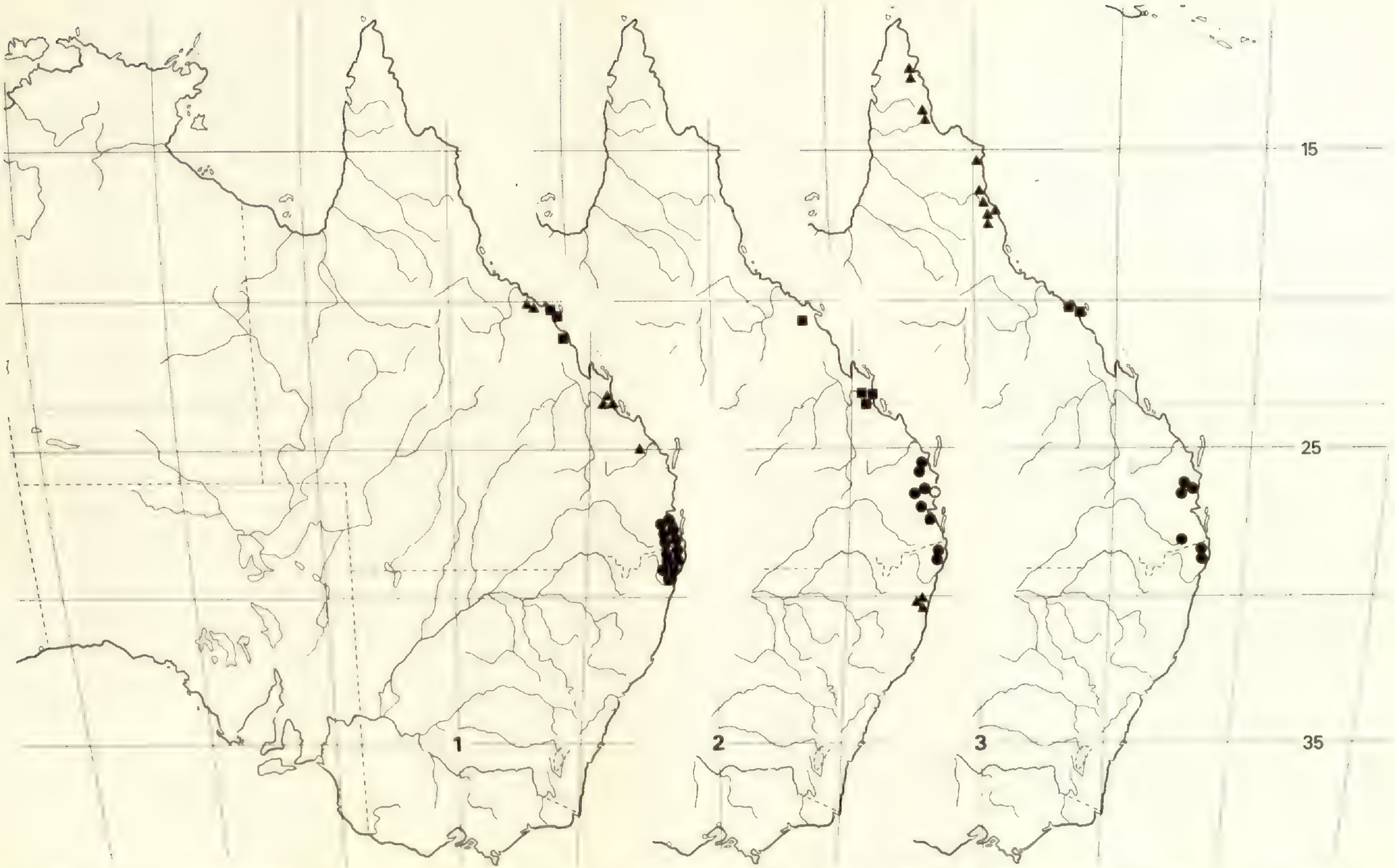
[1] Baillon, in the original description of *Bouchardatia* (Adansonia 7: 351. *t. 10.* 1867), gives the number of ovules per carpel as ". . . usque ad 12." The most I have seen is 8, and the usual number is 6.

ly lobed between the filaments; gynoecium 5-carpellate, carpels basally connate and joined adaxially at about the middle by a single style, otherwise contiguous and forming a 5-lobed ovary, carpels 1-locular, placentation axile, ovules 4–6 per locule, in 2 rows and closely clustered, style straight, composed of 5 stylar elements twisted together, stigma scarcely differentiated from the style. Fruit of 1 or 2, 1-seeded follicles, undeveloped carpels persistent; follicles ellipsoid to obovoid to subglobose, often truncate apically, somewhat compressed laterally, dehiscent along the adaxial and apical edges and partially down the abaxial edge, epicarp dry at maturity, subwoody, endocarp cartilaginous, discharged (probably forcibly) with the seed. Seed ovoid to ellipsoid to reniform; testa brown, smooth, polished, pergamentaceous; endosperm absent; embryo straight or nearly so, cotyledons plano-convex, emarginate at the point of attachment of the hypocotyl, hypocotyl terminal or subterminal.

The bud scales of *Bosistoa* are of a highly specialized type that is generally associated with deciduous trees and shrubs of cold temperate regions of the world. Their presence in this genus of evergreen, tropical and subtropical rain forest trees can probably be taken as evidence that they are vestigial, having been carried over from a time when ancestral populations lived in a cold climate. This immediately suggests that *Bosistoa* may have South American ancestry, and that migrating and evolving populations, during the late Cretaceous and early Tertiary, passed through cold southern latitudes. To my knowledge, however, none of the extant South American genera is very closely related to *Bosistoa*.

I have not seen bud scales of the *Bosistoa* type (i.e., completely enclosing the bud) in any of the other Australasian-Malesian Rutaceae. There are, however, acicular scales associated with the buds of a few of the Australian species described in *Melicope*.

Features of the buds and bud scales of *Bosistoa* are illustrated in FIGURE 1. There are three buds at the shoot apex, one terminal and one in the axil of each of the uppermost pair of leaves. Each bud has two pairs of scales, one outer and one inner. The two scales of each pair are convolute in bud, and the outer pair completely encloses the inner pair. With the opening of the bud and subsequent elongation of the shoot, the scales of the outer pair fall off and those of the inner pair enlarge to form a protective covering for the new leaves or new inflorescence (FIGURE 1b). As the shoot continues to elongate, the enlarged inner bud scales fall off, leaving a pair of overlapping scars where they were attached to the shoot (FIGURE 1c). The fully enlarged inner bud scales (one is shown in FIGURE 1d) lack chlorophyll and range in length from about 2 cm., in *B. brassii*, to about 6 cm., in *B. pentacocca*. In three of the species, *B. pentacocca*, *B. transversa*, and *B. selwynii*, the fully enlarged inner bud scales are remote, in their point of attachment to the shoot, from the scars of the outer pair of scales: in floral shoots they are attached just below the lowermost pair of branches of the inflorescence and in vegetative shoots they are attached about midway between the scars of the outer bud scales and the pair of new leaves. (The remote position of the inner bud scale



MAPS 1–3. Distributions of *Bosistoa* species: 1, *B. pentacocca* (F. Mueller) Baillon var. *pentacocca* (dots), *B. pentacocca* var. *connaricarpa* (Domin) Hartley (triangles), and *B. pentacocca* var. *dryanderensis* Hartley (squares); 2, *B. selwynii* Hartley (dots), *B. floydii* Hartley (triangles), *B. monostylis* (F. M. Bailey) Hartley (circle), and *B. medicinalis* (F. Mueller) Hartley (squares); 3, *B. transversa* Bailey & White (dots), *B. brassii* Hartley var. *brassii* (triangles), and *B. brassii* var. *proserpinensis* Hartley (squares).

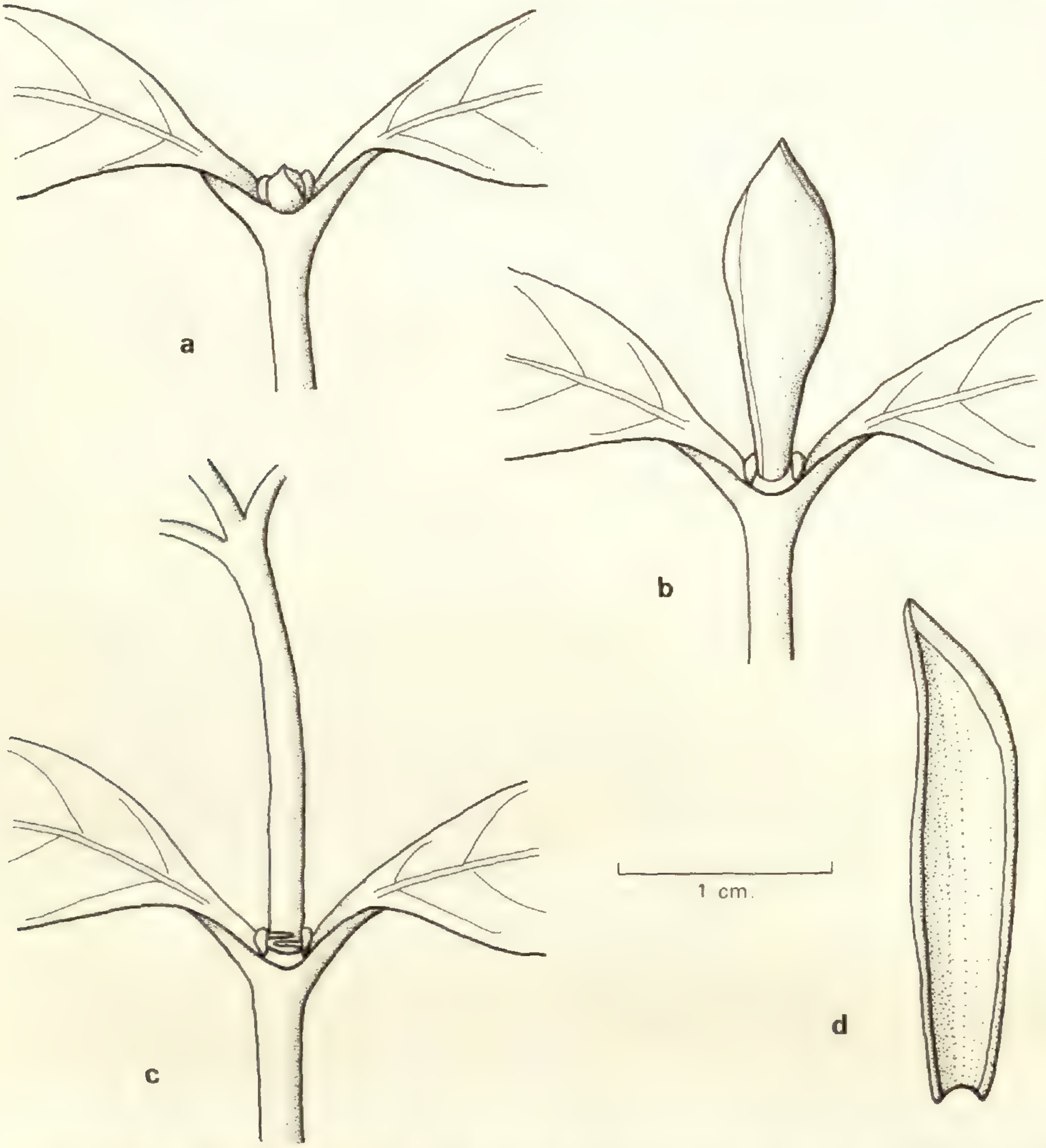


FIGURE 1. Features of buds, bud scales, and bud scale scars of *Bosistoa brassii* Hartley var. *brassii*: a, branchlet apex showing terminal bud and two axillary buds; b, branchlet apex shortly after opening of terminal bud (outer bud scales have fallen, leaving two (one shown) scars; inner pair of bud scales has enlarged and encloses new inflorescence); c, stage after further elongation of inflorescence, showing bases of lowermost pair of branches of inflorescence, and, directly above the scar of an outer bud scale, overlapping scars of caducous inner pair of bud scales; d, fully enlarged inner bud scale fallen from new shoot.

scars of *B. selwynii* is shown in FIGURE 2a.) Also, in these three species, the enlarged inner bud scales usually have minute axillary buds when they are associated with vegetative shoots. They lack such buds, however, when associated with an inflorescence. In a second group of species comprised of *B. floydii*, *B. monostylis*, *B. medicinalis*, and *B. brassii*, the fully enlarged inner bud scales are attached directly above the scars of the outer bud scales (as is shown in FIGURE 1b) and lack, in both vegetative and floral shoots, axillary buds.

Leaf complexity is unusually variable in *Bosistoa,* ranging from imparipinnate to pinnately trifoliolate to unifoliolate. The leaves are consistently imparipinnate in *B. pentacocca* var. *pentacocca* and *B. floydii*; they range from imparipinnate to pinnately trifoliolate in *B. pentacocca* var. *connaricarpa* and *B. pentacocca* var. *dryanderensis*, from pinnately trifoliolate to unifoliolate in *B. transversa*, *B. monostylis*, and *B. medicinalis*; and they are consistently unifoliolate in *B. selwynii* and *B. brassii.*

It seems reasonably certain that the unifoliolate leaf represents a derived condition in the genus and that the imparipinnate leaf is the primitive type. The distal region of the petiole of the unifoliolate leaf is often swollen and/or articulate and thus appears to be homologous with the petiolule (which also may be swollen and is usually articulated with the rachis) of the compound leaf. This apparent retention of the petiolule, or vestiges of it, in the unifoliolate leaf, supports the view that the evolutionary trend in leaf complexity is one of reduction. Such a rudimentary petiolule, as this swollen and/or articulate portion of the petiole might be described, is consistently present in the unifoliolate leaves of *B. transversa* and may or may not be present in the unifoliolate leaves of *B. monostylis* and *B. medicinalis*. The leaves of *B. selwynii* and *B. brassii* have neither swelling nor articulation associated with the petiole, and I am assuming, in describing them as unifoliolate, that they are derived from compound leaves, but that all outward traces of the petiolule have been lost in the course of their evolution.

The terminal inflorescence in *Bosistoa* originates from the middle bud of the three found between the uppermost pair of leaves of the shoot. The two lateral buds of the three may form upper axillary inflorescences, or they may remain dormant during the flowering period and later form vegetative shoots.

As is pointed out above, the species of *Bosistoa* can be divided into two groups based on the relative positions of the inner and outer bud scales in the elongating shoot and on the presence or absence of axillary buds associated with the enlarged bud scales. This classification is given below.

Fully enlarged inner bud scales, or their scars, remote from the scars of the outer bud scales. Axillary buds usually associated with the fully enlarged inner bud scales, or their scars, in vegetative shoots. GROUP I.

1. *B. pentacocca*
2. *B. transversa*
3. *B. selwynii*

Fully enlarged inner bud scales, or their scars, directly above the scars of the outer bud scales. Axillary buds not associated with the fully enlarged inner bud scales, or their scars. GROUP II.

4. *B. floydii*
5. *B. monostylis*
6. *B. medicinalis*
7. *B. brassii*

On the assumption that these are natural groups of species, it appears that the species in Group I represent a comparatively primitive condition in

the genus, because, in having axillary buds, the enlarged inner bud scales of the vegetative shoots are more nearly homologous to true leaves than are those of the species in Group II. The longer internode between the outer and inner bud scales in the elongating shoot of the species in Group I is probably also the primitive condition from which the short internode of the species in Group II was derived.

Within each of the two groups the species are arranged in order of decreasing leaf complexity, following what is quite certainly an evolutionary trend in the genus. Thus, in Group I, the leaves of *Bosistoa pentacocca* (var. *pentacocca*) are imparipinnate, and those of *B. selwynii* are unifoliolate; in Group II, the leaves of *B. floydii* are imparipinnate, and those of *B. brassii* are unifoliolate.

This classification cuts across the traditional line of distinction between *Bosistoa* and *Pagetia*, which was based on differences in leaf complexity (compound, in *Bosistoa*, vs. unifoliolate, or predominantly unifoliolate, in *Pagetia*). *Bosistoa selwynii*, with unifoliolate leaves, is here more closely related to *B. pentacocca*, with pinnately compound leaves, than it is to *B. brassii*, with unifoliolate leaves; and *B. floydii*, with pinnately compound leaves, is more closely related to *B. brassii* than it is to *B. pentacocca*.

KEY TO THE SPECIES

1. Bud scales, at least in younger buds, pubescent; ovary woolly or hispidulous-velutinous; mature follicles densely to rather sparsely pubescent, 0.8–2.5 cm. wide.
   2. Leaves unifoliolate. ..... 3. *B. selwynii.*
   2. Leaves, or at least some of them, compound.
      3. Scars of inner pair of bud scales directly above those of outer pair; ovary hispidulous-velutinous; mature follicles sparsely pubescent, 0.8–1 cm. wide. ..... 4. *B. floydii.*
      3. Scars of inner pair of bud scales remote from those of outer pair; ovary woolly; mature follicles densely and minutely pubescent, 1–2.5 cm. wide.
         4. Petals glabrous abaxially; leaves imparipinnate or pinnately trifoliolate; follicles 1.5–2.5 cm. wide. ..... 1. *B. pentacocca.*
         4. Petals pubescent abaxially; leaves pinnately trifoliolate or occasional leaves unifoliolate; follicles about 1 cm. wide. ..... 2. *B. transversa.*
1. Bud scales glabrous; ovary sparsely and minutely hispidulous, sparsely villous, or glabrous; mature follicles, where known, glabrous, 0.8–1 cm. wide.
   5. Ovary sparsely and minutely hispidulous; leaves unifoliolate or occasional leaves trifoliolate. ..... 6. *B. medicinalis.*
   5. Ovary sparsely villous to glabrous.
      6. Leaves trifoliolate or occasional leaves unifoliolate. ..... 5. *B. monostylis.*
      6. Leaves unifoliolate. ..... 7. *B. brassii.*

1. Bosistoa pentacocca (F. Mueller) Baillon, Hist. Pl. 4: 470. 1873.

Three nearly allopatric varieties are recognized in this species (see MAP 1).

KEY TO THE VARIETIES

1. Leaflet margin usually crenate or serrate, main veins 16–30 on each side of the midrib.
   2. Leaves imparipinnate, 14–45 cm. long; leaflets (3–)4–5(–6) pairs. ..... 1a. var. *pentacocca*.
   2. Leaves imparipinnate or pinnately trifoliolate, 9–30 cm. long; leaflets 1–2 pairs. ..... 1b. var. *connaricarpa*.
1. Leaflet margin entire, main veins 13–16 on each side of the midrib. ..... 1c. var. *dryanderensis*.

1a. Bosistoa pentacocca (F. Mueller) Baillon var. pentacocca.

Euodia pentacocca F. Mueller, Frag. Phytogr. Austral. 3: 41. 1862. TYPE: *Beckler*, New South Wales, Clarence River.

Bosistoa sapindiformis F. Mueller ex Bentham, Fl. Austral. 1: 359. 1863, *nomen illegit.*, based on *Euodia pentacocca* F. Mueller.

Acradenia bosistoi F. Mueller, Pap. Proc. Roy. Soc. Tasmania 8: 8. 1868, and Frag. Phytogr. Austral. 6: 167. 1868, *nomen illegit.*, based on *Euodia pentacocca* F. Mueller.

Small to medium tree to about 18 m.; branchlets densely pubescent in new growth, becoming glabrous; buds pubescent; scars of inner pair of bud scales remote from those of outer pair. Leaves imparipinnate, 14–45 cm. long; petiolules of lateral leaflets obsolete to 8 mm. long, terminal leaflet on an extension of the rachis 5–25 mm. long; leaflets (3–)4–5(–6) pairs, chartaceous to subcoriaceous, glabrous, elliptic-oblong to narrowly elliptic or (most terminal leaflets) oblanceolate, 9–27 cm. long, 1.5–7 cm. wide, base acute to obtuse or occasionally rounded, margin crenate to coarsely and bluntly serrate, apex acuminate, the acumen to 4 cm. long, main veins 20–30 on each side of the midrib. Inflorescence terminal, (10–)15–20(–33) cm. long, peduncle and lower axis densely pubescent, upper axis and branches sparsely and finely pubescent. Flowers 4.5–5.5 mm. long; sepals glabrous or nearly so, connate, forming a minutely 5-lobed calyx cup about 1 mm. high, persistent in fruit; petals glabrous, broadly oblanceolate, about 4.5 mm. long; stamens with narrowly lanceolate filaments, anthers about 1.5 mm. long; disc glabrous, columnar, about 0.7 mm. high; ovary woolly, about 1.5 mm. high, ovules 4 per locule; style glabrous, 2–2.5 mm. long. Follicles subglobose to ellipsoid, 1.5–2.5 cm. wide; exocarp densely and minutely pubescent, wrinkled and often transversely ribbed. Seed subellipsoid, 15–20 mm. long.

ILLUSTRATIONS. Engler, A., Nat. Pflanzenfam. III. 4: 113. *fig. 64J.* 1896 (flower only). *Ibid.* ed. 2. 19a: 215. *fig. 92J.* 1931 (flower only).

DISTRIBUTION. Southeast Queensland and northeast New South Wales; rain forests, often along streams. See MAP 1.

Queensland. MORETON DISTRICT: Moreton Bay, Mr. Cameron's Brush, *Leichhardt*, March 13, 1844 (NSW 128894, P); Ipswich, *Nernst* (K, MEL); Pimpama, *Herb. Simmonds*, March 18, 1889 (BRI); Coomera, *Scortechini 168* (MEL); Logan

River, *Scortechini* (BRI); Tamborine Mt., *Blake 17387* (BRI), *Shirley*, February, 1917 (A, BRI); Kalbar, *Smith*, September, 1935 (BRI); Beech Mountain [probably Beechmont or Beechmont Range], *White 1912* (A, BRI, NSW, P); upper Albert River, *White 10370* (A, BM); Canungra, *Boorman*, April, 1907 (NSW 128904, W); Lamington National Park, *Shirley*, March, 1909 (NSW 128903). **New South Wales.** Tweed River near Mt. Warning, *Anonymous 63* (MEL); Tweed Valley, Limpinwood Faunal Reserve, near Chillingham, *Williams*, May 31, 1965 (COFFS HARBOUR); Mt. Warning, *Boorman*, August, 1916 (BRI, NSW 128899, US), *Fraser*, January 16, 1936 (NSW 128906); Lynches Creek, *Hayes*, May 8, 1954 (COFFS HARBOUR); Mebbin State Forest, *Floyd & Hayes*, January 23, 1958 (COFFS HARBOUR), *Lemaire*, September 17, 1965 (COFFS HARBOUR); 3.2 km. SW of Wiangaree, *Hayes, Turner, & McGillivray 2554* (NSW); Toonumbar, *Hayes*, 1954 (COFFS HARBOUR); Whian Whian State Forest, *de Beuzeville LXVII* (A, NSW); north arm of Richmond River, *Anonymous* (MEL); Byron Creek, Booyong Creek, *Johnson & Constable*, June 11, 1957 (NSW 128890); Wilson's Creek, *Anonymous 19* (NSW); rain forest reserve near Booyong, *Johnson, Constable, & Hayes*, June 11, 1957 (COFFS HARBOUR); Lismore, *Anonymous*, January, 1894 (CAL, NSW 135636, US), *Baeuerlen*, June, 1891 (A, NSW 135632), *Forest Guard*, March, 1909 (L, NSW 135635), April, 1909 (NSW 128895), August 27, 1909 (NSW 135633, PR), October 18, 1909 (BISH, UC), *Rothwell*, November, 1906 (NSW 128893); Tintenbar, *Baeuerlen*, October, 1893 (NSW 128891, U); Casino, *Rummey*, August, 1916 (NSW 128892); Richmond River, *Henderson 156* (MEL); Tweed and Richmond Rivers, *Anonymous 66* (MEL); Ballina, *Anonymous*, February, 1894 (MEL); Clarence River, *Beckler* (MEL, holotype of *Euodia pentacocca* F. Mueller; K, isotype).

1b. **Bosistoa pentacocca** (F. Mueller) Baillon var. **connaricarpa** (Domin) Hartley, comb. & stat. nov.

Bosistoa connaricarpa Domin, in Feddes Repert. **12:** 390. 1913, and Bibliot. Bot. **22**(89): 288. 1927. TYPE: *Dallachy*, February 5, 1863, Queensland, Rockhampton.

Small tree; branchlets finely pubescent in new growth, becoming glabrous; buds pubescent; scars of inner pair of bud scales remote from those of outer pair. Leaves imparipinnate or pinnately trifoliolate, 9–30 cm. long; petiolules of lateral leaflets 1–6 mm. long, extension of the rachis subtending terminal leaflet obsolete to 33 mm. long; leaflets 1 or 2 pairs, subcoriaceous, glabrous, oblanceolate or occasionally elliptic or narrowly elliptic, 4.5–22 cm. long, 2–9 cm. wide, base cuneate to acute or obtuse, occasionally oblique in lateral leaflets, margin crenate to coarsely and bluntly serrate or occasionally entire, apex acuminate, the acumen to 1.5 cm. long, main veins 16–24 on each side of the midrib. Inflorescences terminal or terminal and from the axils of upper leaves, 5–10 cm. long, peduncle and branches rather sparsely and finely pubescent. Flowers about 4 mm. long; sepals glabrous, basally connate, triangular, about 0.7 mm. long, persistent in fruit; petals glabrous, subelliptic, about 3.5 mm. long; stamens with sublinear filaments, anthers 1.2 mm. long; disc glabrous, columnar, about 0.5 mm. high; ovary woolly, about 1.5 mm. high, ovules

4 per locule; style glabrous, about 1 mm. long. Follicles truncately subglobose, 1.8–2.3 cm. wide; exocarp densely and minutely pubescent, wrinkled. Seed not seen.

DISTRIBUTION. East central Queensland, from Bowen south to Gin Gin; rain forests. See MAP 1.

Queensland. NORTH KENNEDY DISTRICT: Port Denison [Bowen], *Fitzalan*, 1874 (L, MEL); Edgecumbe Bay, *Anonymous* (W). PORT CURTIS DISTRICT: Mt. Archer [at Rockhampton], *Anonymous* (MEL); Fitzroy River, *O'Shanesy 86 ser. 9* (MEL); Rockhampton, *Anonymous* (BM, L, P, U), *Herb. Hance 10552* (BM, P), *Dallachy*, February 5, 1863 (MEL, isotype of *Bosistoa connaricarpa* Domin), *Thozet* (GH, MEL, P). WIDE BAY DISTRICT: Gin Gin, *Scortechini 305* (MEL).

1c. Bosistoa pentacocca (F. Mueller) Baillon var. dryanderensis Hartley, var. nov.

Arbor parva usque ca. 10 m. alta; ramulis glabratis; gemmis pubescentibus; cicatricibus perularum interiorum delapsarum ex cicatricibus perularum exteriorum delapsarum remotis; foliis imparipinnatis, 1–2-jugis, 14–28 cm. longis; petiolulis foliolorum lateralium obsoletis vel usque 4 mm. longis, rhachidi ad apicem extensa 10–25(–40) mm. longa foliolum terminale ferente; foliolis subcoriaceis vel coriaceis, glabris, anguste vel late ellipticis vel oblanceolatis vel obovatis, 8–20 cm. longis, 2.5–7.5 cm. latis, basi acutis vel obtusis vel cuneatis, plerumque inaequilateribus in foliolis lateralibus, margine integris, apice acuminatis, acumine usque 2.5 cm. longo, venis primariis utrinsecus costa 13–16; inflorescentiis terminalibus vel terminalibus et ex axillis foliatis superioribus orientibus, 10–23 cm. longis, pedunculo sparse et subtiliter pubescentibus, ramis puberulis; floribus (visi tantum in alabastro) ca. 4 mm. longis; calyce glabro, cupulato, ca. 1 mm. alto, minute 5-lobato, in fructu persistenti; petalis glabris; staminibus filamentis sublinearibus, antheris 1–1.3 mm. longis; disco glabro, columnari, ca. 0.5 mm. alto; ovario lanato, ca. 1 mm. alto, ovulis in quoque loculo 4; stylo glabro, ca. 2 mm. longo; folliculis truncate obovoideis, 1.5–1.7 cm. latis; exocarpio dense et minute pubescenti, rugoso; semine subreniformi, ca. 10 mm. longo. HOLOTYPUS: *Moriarty 968* (CANB).

DISTRIBUTION. East central Queensland, in the vicinity of Mt. Dryander and at Mackay; rain forests to about 150 meters. See MAP 1.

Queensland. NORTH KENNEDY DISTRICT: Mt. Dryander, *Jones 3216* (CANB), *Kilmer & Fitzalan* (MEL), *Michael 708, in part* (GH), *Moriarty 968* (CANB, holotype; BRI, isotype), *Webb & Tracey 10067* (BRI); State Forest Reserve 299, Conway Logging Area, *Hyland RFK 4071* (CANB), *RFK 4072* (CANB); Mt. Marlow, *Michael 708, in part* (BRI). SOUTH KENNEDY DISTRICT: Mackay, *Nugent 11* (BRI). Without definite locality: *Macpherson 122* (*North Qld. Herb. 4409*) (QRS).

2. Bosistoa transversa Bailey & White, Queensl. Dept. Agr. Bot. Bull. 19: 7. *t.* 2. 1917. LECTOTYPE (chosen here): *Francis & White*, March, 1916, Queensland, Kin Kin.

Small to medium tree to about 15 m.; branchlets glabrous or nearly so; buds pubescent (sometimes sparsely); scars of inner pair of bud scales remote from those of outer pair. Leaves pinnately trifoliolate (occasional leaves bifoliolate or unifoliolate), 8.5–16 cm. long; petiolules of lateral leaflets obsolete to 5 mm. long, terminal leaflet on an extension of the rachis 8–25 mm. long, petioles of unifoliolate leaves 5–12 mm. long; leaflets subcoriaceous to coriaceous, glabrous, elliptic-oblong to broadly elliptic, 4–12.5 cm. long, 1–6 cm. wide, base cuneate to rounded, usually oblique in lateral leaflets, margin entire, apex bluntly acuminate (the acumen to 2 cm. long) or occasionally acute or obtuse, main veins 9–12 on each side of the midrib. Inflorescences terminal or terminal and from the axils of upper leaves, 7–16 cm. long, peduncle and branches finely pubescent to puberulent. Flowers about 3.5 mm. long; sepals pubescent, basally connate, triangular, 0.7–1 mm. long, persistent in fruit; petals pubescent abaxially, sparsely pubescent adaxially, broadly elliptic, about 3 mm. long; stamens with sublinear filaments, anthers about 1 mm. long; disc glabrous, pulvinate, about 0.3 mm. high; ovary woolly, about 0.7 mm. high, ovules 4 per locule; style pubescent toward the base, glabrous above, about 1.2 mm. long. Follicles obovoid, 1–1.3 cm. wide; exocarp densely and minutely pubescent, transversely ribbed. Seed reniform, about 10 mm. long.

ILLUSTRATION. J. F. Bailey & C. T. White, *loc. cit.*

DISTRIBUTION. Southeast Queensland and northeast New South Wales; rain forests to 150 meters. See MAP 2.

Queensland. WIDE BAY DISTRICT: Kin Kin, *Francis*, May, 1919 (A, BM), *Francis & White*, March, 1916 (BRI, lectotype), *White*, January, 1917 (BM, BRI, CANB); Imbil, State Forest Reserve 256, Mitchell Logging Area, *Moriarty 1641* (BRI, CANB); Imbil, *Deputy Forester Cochrane*, July 25, 1923 (BRI), *Dun*, 1950 (COFFS HARBOUR), *Jones 3288* (CANB), *King*, 1949 (COFFS HARBOUR), *Smith & Webb 3121* (BRI, NY). MORETON DISTRICT: Eumundi, *Bailey*, May, 1892 (BRI), May 1, 1896 (BRI), *Herb. Simmonds*, January, 1892 (BRI). DARLING DOWNS DISTRICT: Gladfield, *Bailey* (NSW 128897). **New South Wales.** Tweed River, *Moore 212* (K); Mullimbimby, Tongoggin Mt., *Baeuerlen*, February, 1895 (NSW).

The lectotype is one of two collections (the other being *Bailey*, May, 1892, from Eumundi) cited in the original description of *Bosistoa transversa*.

Collectors have sometimes confused *Bosistoa transversa* with *Bouchardatia neurococca* (F. Mueller) Baillon, and Francis (Austral. Rain-forest Trees. ed. 3. 175. 1970) expressed doubt that the two can be separated. A good spot character for the recognition of *Bouchardatia* is found in the presence of domatia in its leaves. This and other distinguishing features of the two genera are given in the introductory part of this paper.

FIGURE 2. *Bosistoa selwynii* Hartley: a, flowering branchlet, showing pronounced venation of lower surface of four leaves (note remote position of inner bud scale scars (arrows) on vegetative shoots and inflorescence); b, flower with one stamen removed (both drawn from *Moriarty 1644*).

3. **Bosistoa selwynii** Hartley, sp. nov. FIGURE 2.

Arbor parva vel mediocris usque ca. 22 m. alta; ramulis glabratis; gemmis pubescentibus; cicatricibus perularum interiorum delapsarum ex cicatricibus perularum exteriorum delapsarum remotis; foliis unifoliolatis, 5.5–13.5 cm. longis; petiolo obsoleto vel usque 8 mm. longo; foliolo subcoriaceo vel coriaceo, omnino glabro vel subtus subtiliter et sparse pubescenti, ovato vel elliptico vel interdum suborbiculari, 5–13 cm. longo, 2.5–9 cm. lato, basi cordato vel interdum acuto, obtuso, vel rotundato, aequilatero, margine integro, apice acuto vel rotundato vel interdum acuminato, acumine usque 1.5 cm. longo, venis primariis utrinsecus costa 9–12; inflorescentiis terminalibus vel terminalibus et ex axillis foliatis superioribus orientibus, 6–10 cm. longis, pedunculo et ramis subtiliter pubescentibus; floribus 4–5.5 mm. longis; sepalis pubescentibus, basaliter connatis, triangularibus, 0.8–1.5 mm. longis, in fructu persistentibus; petalis abaxialiter pubescentibus, adaxialiter sparse pubescentibus, late ellipticis, 3.5–4.5 mm. longis; staminibus filamentis sublinearibus, antheris 0.8–2 mm. longis; disco glabro, pulvinato, 0.5–1 mm. alto; ovario lanato, 1–1.5 mm. alto, ovulis in quoque loculo 4; stylo sparse pubescenti, 1.5–3 mm. longo; folliculis truncate obovoideis, ca. 1 cm. latis; exocarpio dense et minute pubescenti, transverse costato; semine subreniformi, ca. 10 mm. longo. HOLOTYPUS: *Moriarty 1644* (CANB).

DISTRIBUTION. Southeast Queensland and northeast New South Wales; rain forests to 300 meters. See MAP 2.

Queensland. WIDE BAY DISTRICT: Maryborough District, *Petrie 8a* (BRI); Oakview [near Kilkivan], Forest Reserve 220, Sinai, *Forest Overseer Reynolds*, April 18, 1923 (BRI); Imbil, *Deputy Forester Cochrane* (BRI), *Fraser 134* (BRI); Imbil, State Forest Reserve 135, Little Derrier Logging Area, *Moriarty 1642* (BRI, CANB), *1643* (CANB), *1644* (CANB, holotype; BRI, isotype); near Imbil, *Smith & Webb 3134* (BRI, CANB). MORETON DISTRICT: Kilcoy, *England*, March, 1937 (BRI); Mt. Glorious, Cedar Creek, *White 1940* (A, BO, BRI, NSW, US). **New South Wales.** Limpinwood Nature Reserve, Oxley River, *Floyd*, November 26, 1976 (COFFS HARBOUR); Whian Whian State Forest, about 24 km. N of Lismore, *Smith 5137* (BRI).

Collectors have confused this species, *Bosistoa selwynii*, with *Pagetia dietrichiae* Domin, apparently because the latter was originally described as having been collected from near Brisbane. As is pointed out below under *Bosistoa medicinalis*, the syntypes of *Pagetia dietrichiae* probably all came from the vicinity of Rockhampton.

This species is named in honor of Selwyn L. Everist, former director of the Queensland Herbarium and authority on Australian poisonous plants.

4. **Bosistoa floydii** Hartley, sp. nov. FIGURE 3.

Arbor mediocris usque ca. 15 m. alta; ramulis glabris; gemmis pubescentibus; cicatricibus perularum interiorum delapsarum ex cicatricibus perularum exteriorum delapsarum proxime super; foliis imparipinnatis, 2-jugis (saepe

FIGURE 3. *Bosistoa floydii* Hartley: a, fruiting branchlet, two axillary shoots removed from lower node (drawn from *Floyd*, February 25, 1975); b, flower, three stamens removed (drawn from *Floyd*, October 21, 1974).

foliolis duo adjectis redactis reflexis in nodo infimo), 11–28 cm. longis; petiolulis foliolorum lateralium obsoletis vel usque 8 mm. longis, rhachidi ad apicem extensa 1–13 mm. longa foliolum terminale ferente; foliolis subcoriaceis, glabris, anguste ellipticis vel ellipticis, 8–16 cm. longis, 2–5 cm. latis (foliolis redactis, quum praesentibus, 4–6.5 cm. longis, 0.7–1.5 cm. latis), basi cuneatis vel attenuatis, saepe inaequilateris in foliolis lateralibus, margine integris, apice acuminatis, acumine usque 3 cm. longo, venis primariis utrinsecus costa 16–20; inflorescentia terminali, 10–16 cm. longa, pedunculo glabro vel fere glabro, ramis sparse et minute pubescentibus; floribus 5–6 mm. longis; sepalis margine ciliatis, aliter glabris, basaliter connatis, triangularibus, ca. 1 mm. longis, in fructu persistentibus; petalis glabris, oblanceolatis, 4–5 mm. longis; staminibus filamentis linearibus, antheris ca. 1 mm. longis; disco glabro, pulvinato, 0.5–0.6 mm. alto; ovario sparse vel dense hispidulo-velutino, ca. 1 mm. alto, ovulis in quoque loculo 5; stylo glabro, ca. 2 mm. longo; folliculis oblique obovoideis vel subglobosis, 0.8–1 cm. latis; exocarpio sparse pubescenti, transverse costato; semine late ellipsoideo, ca. 7 mm. longo. HOLOTYPUS: *Floyd*, February 25, 1975 (CANB).

DISTRIBUTION. Northeast New South Wales, vicinity of Dorrigo and Coffs Harbour; rain forests. See MAP 2.

New South Wales. Upper Orara River, *Floyd*, February 23, 1974 (COFFS HARBOUR); Miram Creek, upper Orara River, *Floyd*, October 21, 1974 (COFFS HARBOUR), February 25, 1975 (CANB, holotype); Dorrigo, *Fraser*, January, 1935 (NSW 128907); Dorrigo Forest Reserve, *Anonymous*, October 6, 1896 (NSW 128901); Dorrigo Mountain Park, *Floyd*, November 17, 1958 (COFFS HARBOUR); Dorrigo National Park, *Williams*, December, 1962 (NSW 128900); Oakes State Forest, *Hayes*, January 17, 1962 (COFFS HARBOUR).

As is pointed out above, *Bosistoa floydii* and the next three species, *B. monostylis*, *B. medicinalis*, and *B. brassii*, appear to be more closely related to one another than they are to the other three species of the genus. Beyond this, *B. monostylis*, *B. medicinalis*, and *B. brassii* seem to be closely interrelated, but *B. floydii*, which is very different in its leaf characteristics, is quite distinct.

5. **Bosistoa monostylis** (F. M. Bailey) Hartley, comb. nov.

Pagetia monostylis F. M. Bailey, Queensl. Dept. Agr. Bot. Bull. 13: 7. 1895. TYPE: *F. M. Bailey* (*Field Naturalists' Excursion*), November, 1895, Queensland, Eumundi.

Medium tree to about 18 m.; branchlets glabrous; buds glabrous; scars of inner pair of bud scales directly above those of the outer pair. Leaves pinnately trifoliolate (occasional leaves unifoliolate), 8.5–13 cm. long; lateral leaflets sessile or subsessile, terminal leaflet on an extension of the rachis 10–17 mm. long, petioles of unifoliolate leaves 10–20 mm. long; leaflets subcoriaceous, glabrous, elliptic, 7–9.5 cm. long, 2–4 cm. wide, base acute to obtuse, oblique in lateral leaflets, margin entire, apex bluntly acuminate, the acumen to 1 cm. long, main veins 12–15 on each side of the midrib. Inflorescences terminal or terminal and from the axils of upper leaves, 7–10 cm. long, peduncle and axis glabrous, upper branches puberulent. Flowers about 5 mm. long; sepals ciliate at the margin, otherwise glabrous, basally connate, ovate to triangular, about 1 mm. long; petals puberulent abaxially, glabrous adaxially, elliptic, about 4 mm. long; stamens with sublinear filaments, anthers about 1 mm. long; disc glabrous, pulvinate, about 0.5 mm. high; ovary sparsely villous toward the apex, otherwise glabrous, about 1 mm. high, ovules 4 per locule; style glabrous, about 1.5 mm. long. Follicles not seen.

ILLUSTRATION. F. M. Bailey, Comprehensive Cat. Queensl. Pl. 80. *t. 61.* 1909.

DISTRIBUTION. Known definitely only from the type locality; rain forest. See MAP 2.

Queensland. MORETON DISTRICT: Eumundi, *Bailey* (*Field Naturalists' Excursion*), November, 1895 (BRI, holotype of *Pagetia monostylis* F. M. Bailey; NSW 135603, W, isotypes), *Simmonds*, November, 1895 (BRI, MEL, NSW 135602).

The style in *Bosistoa* is composed of five separate stylar elements which are tightly twisted together and are fused apically into a common, more or less undifferentiated stigma. This is a common structure in the Rutaceae and is usually referred to as a single style with a single stigma. Mueller, however, when publishing the genus *Pagetia*, of which *Bosistoa medicinalis* is the type species, described it as follows: "Styli 5 breves, in unicum contorti. Stigmata minuta, coalita." This seems to be just another way of describing the same structure, but it led Bailey to choose the epithet *monostylis* for the present species.

Bosistoa monostylis and *B. medicinalis* are very similar morphologically, and it is with some hesitation that I have decided to recognize them as distinct species. In flower they can be distinguished by the trichomes on the ovary, which are long and more or less flexuous in *B. monostylis* and short and stiff in *B. medicinalis*. In fruiting specimens of the latter species (and probably in the former as well, since there is no reason to suspect that its fruit, which has not been collected, is other than typical for the genus), the nature of this pubescence can generally be determined because it persists for some time on the undeveloped carpels. (As is noted in the generic description, only one or two of the five carpels develop into fruits, and the undeveloped ones are persistent.) Sterile specimens can generally be determined to species by their leaf complexity, which is predominantly trifoliolate in *B. monostylis* and predominantly or entirely unifoliolate in *B. medicinalis*. Nevertheless, there are some predominantly or entirely unifoliolate sterile collections that I have preferred to determine as *B.* cf. *monostylis*. They are the following:

Queensland. PORT CURTIS DISTRICT: Fitzroy River, *Anonymous* (BO, CAL, L, MEL); Mt. Archer, *Tracey* (CANB). WIDE BAY DISTRICT: Wide Bay, Mr. Archer's Brush, *Leichhardt* (MEL).

Luerssenidendron monostylis Domin, described from northeast New South Wales, has been incorrectly referred to *Pagetia monostylis* (see below under Excluded Species).

6. Bosistoa medicinalis (F. Mueller) Hartley, comb. nov.

Pagetia medicinalis F. Mueller, Frag. Phytogr. Austral. **5**: 178. 1866. LECTOTYPE (chosen here): *O'Shanesy 247*, Queensland, Rockhampton.
Pagetia dietrichiae Domin, Bibliot. Bot. **22**(89): 291. 1927. SYNTYPES: *Dietrich 643*, *1544*, *1768*, and *2212*, Queensland. Brisbane River [probably Rockhampton — see discussion below].

Small to medium tree to about 20 m.; branchlets glabrous; buds glabrous; scars of inner pair of bud scales directly above those of outer pair. Leaves unifoliolate (occasional leaves pinnately trifoliolate or bifoliolate), 5–18 cm. long; petiole 4–10(–15) mm. long (in compound leaves lateral leaflets sessile or subsessile, terminal leaflet on an extension of the rachis 3–14 mm. long); leaflets subcoriaceous to coriaceous, glabrous, obovate to elliptic, ovate, or suborbicular, 5–17 cm. long, 2–8.5 cm. wide (in com-

pound leaves elliptic to narrowly obovate to oblanceolate, 3.5–8.5 cm. long, 1.5–3 cm. wide), base acute to cordate, equal-sided (in compound leaves acute to cuneate, oblique in lateral leaflets), margin entire, apex obtuse to acuminate, the acumen to 1.5 cm. long, main veins 10–13 on each side of the midrib. Inflorescences terminal or terminal and from the axils of upper leaves, 5–8 cm. long, peduncle and axis glabrous, branchlets puberulent. Flowers about 5 mm. long; sepals finely pubescent, ciliate at the margin, basally connate, ovate to triangular, about 1 mm. long, deciduous in fruit; petals puberulent abaxially, glabrous adaxially, broadly elliptic, about 4.5 mm. long; stamens with sublinear filaments; anthers 1–1.5 mm. long; disc glabrous, pulvinate, about 0.5 mm. high; ovary rather sparsely and minutely hispidulous, about 1 mm. high, ovules 4 per locule; style glabrous, about 1.5 mm. long. Follicles obovoid to subglobose, about 1 cm. wide; exocarp becoming glabrous, transversely ribbed. Seed subreniform, about 8 mm. long.

DISTRIBUTION. East central Queensland, vicinities of Proserpine and Rockhampton (see discussion below); rain forests. See MAP 2.

Queensland. NORTH KENNEDY DISTRICT: Kelsey Creek, [near] Proserpine, *Thorogood 7* (BRI). PORT CURTIS DISTRICT: Rockhampton, *Dietrich 643* (HBG, PR), *1436* (MEL), *1544* (HBG, MEL, NY, PR), *1768* (HBG, PR), *2212* (HBG, MEL, PR), *O'Shanesy 247* (MEL, lectotype of *Pagetia medicinalis* F. Mueller), *Thozet*, 1878 (P); Crocodile Creek [near Rockhampton], *Bowman* (MEL); Mt. Buzzard [near Rockhampton], *Dallachy* (MEL).

Of the collections cited above, those of O'Shanesy, Thozet, Bowman, and Dallachy are syntypes cited by Mueller with the original description of *Pagetia medicinalis*. I have chosen the sheet of the O'Shanesy collection as the lectotype.

As interpreted here, *Bosistoa medicinalis* is extremely variable in leaf complexity and leaflet shape. The syntypes of *Pagetia dietrichiae* Domin fall well within this range of variability.

Domin was at least partially misled when he gave the locality of *Pagetia dietrichiae* as Brisbane River. The Dietrich collections he cited had been distributed with printed labels that gave the locality as "prope Brisbane River," but the Hamburg and New York sheets of *Dietrich 1544* now have a photocopy of a label, in Dietrich's handwriting, giving the locality as Rockhampton. Also, the Melbourne sheets of *Dietrich 1544* and *2212* have labels (but not in Dietrich's handwriting) giving the locality as Rockhampton. In correspondence with the Hamburg herbarium, we have learned that in Dietrich's catalog of collections there is no locality given for numbers *643*, *1768*, and *2212*, but that numbers *633–637*, *650–733*, *1767*, and *2213* were all collected at Rockhampton, and that number *644* was collected at Mackay. There is no reliable evidence that any of the syntypes of *P. dietrichiae* were collected from the Brisbane River. It is probably worth noting that all four of the syntype collections, and *Dietrich 1436*, which was not cited by Domin, are at the same stage of flowering and otherwise appear to be identical. I think it is likely that they were all collected from the same tree on the same date.

According to Mueller, the oil from the leaves of this species has been used therapeutically; hence his choice of the epithet *medicinalis*.

7. **Bosistoa brassii** Hartley, sp. nov.

Two allopatric varieties are recognized in this species.

Key to the Varieties

1. Petiole 3–10 mm. long; leaflet cuneate or occasionally acute to obtuse at the base; ovary sparsely villous. ..... 7a. var. *brassii*.
1. Petiole 1–2.5 mm. long; leaflet obtuse to rounded to subcordate at the base; ovary glabrous. ..... 7b. var. *proserpinensis*.

7a. **Bosistoa brassii** Hartley var. **brassii**. FIGURE 4.

Arbor parva vel mediocris usque ca. 18 m. alta; ramulis glabris; gemmis glabris; cicatricibus perularum interiorum delapsarum ex cicatricibus perularum exteriorum delapsarum proxime super; foliis unifoliolatis, 6.5–19 cm. longis; petiolo 3–10 mm. longo; foliolo subcoriaceo, glabro, elliptico vel obovato, 7–18.5 cm. longo, 3.5–9 cm. lato, basi cuneato vel interdum acuto vel obtuso, aequilatero, margine integro, apice acuminato, acumine usque 1.5 cm. longo, venis primariis utrinsecus costa 10–16; inflorescentiis terminalibus vel terminalibus et ex axillis foliatis superioribus orientibus, 5–9 cm. longis, pedunculo glabro vel fere glabro, ramulis glabris vel subtiliter pubescentibus; floribus 5–6 mm. longis; sepalis margine ciliatis, aliter glabris, distinctis vel basaliter connatis, anguste triangularibus, ca. 1 mm. longis, in fructu deciduis; petalis abaxialiter apicem versus puberulis, adaxialiter glabris, ellipticis, 4–4.5 mm. longis; staminibus filamentis linearibus, antheris 0.7–0.8 mm. longis; disco glabro, pulvinato, 0.4–0.6 mm. alto; ovario sparse villoso, ca. 1 mm. alto, ovulis in quoque loculo 4; stylo glabro, ca. 2 mm. longo; folliculis subglobosis, ca. 0.8 cm. latis; exocarpio glabro, transverse costato; semine ovoideo, ca. 8 mm. longo. HOLOTYPUS: *Brass 19653* (CANB).

DISTRIBUTION. North Queensland, from the Cape York Peninsula south to the Atherton Tableland; rain forests, often along streams; sea level to about 600 meters. See MAP 3.

Queensland. COOK DISTRICT: Pascoe River, Horse Creek, *Hyland 6435* (CANB); West Claudie River, *Hyland 6180* (CANB); Claudie River, *Hyland RFK 2708* (QRS); Iron Range, *Brass 19653* (CANB, holotype; L, isotype); McIlwraith Range, *Smith 11831* (BRI, L); Rocky River, *Hyland RFK 2555* (BRI, QRS); Mt. Cook, near Cooktown, *Smith 10593* (BRI), *Webb & Tracey 7048* (BRI); Mossman Gorge, *Hyland RFK 1129* (QRS), *Webb & Tracey 7047* (BRI); Forest Reserve 1073, Smithfield, N of Kuranda, *Dansie 1935 (QF 62/41)* (BRI); Crystal Cascades, near Cairns, *Webb & Tracey 8194* (BRI); Yarrabah, *Michael 435* (BRI, GH, NSW); above Copperlode Falls Dam Site, *Stocker 976* (CANB); State Forest Reserve 607, Lock Logging Area, *Irvine 758* (CANB).

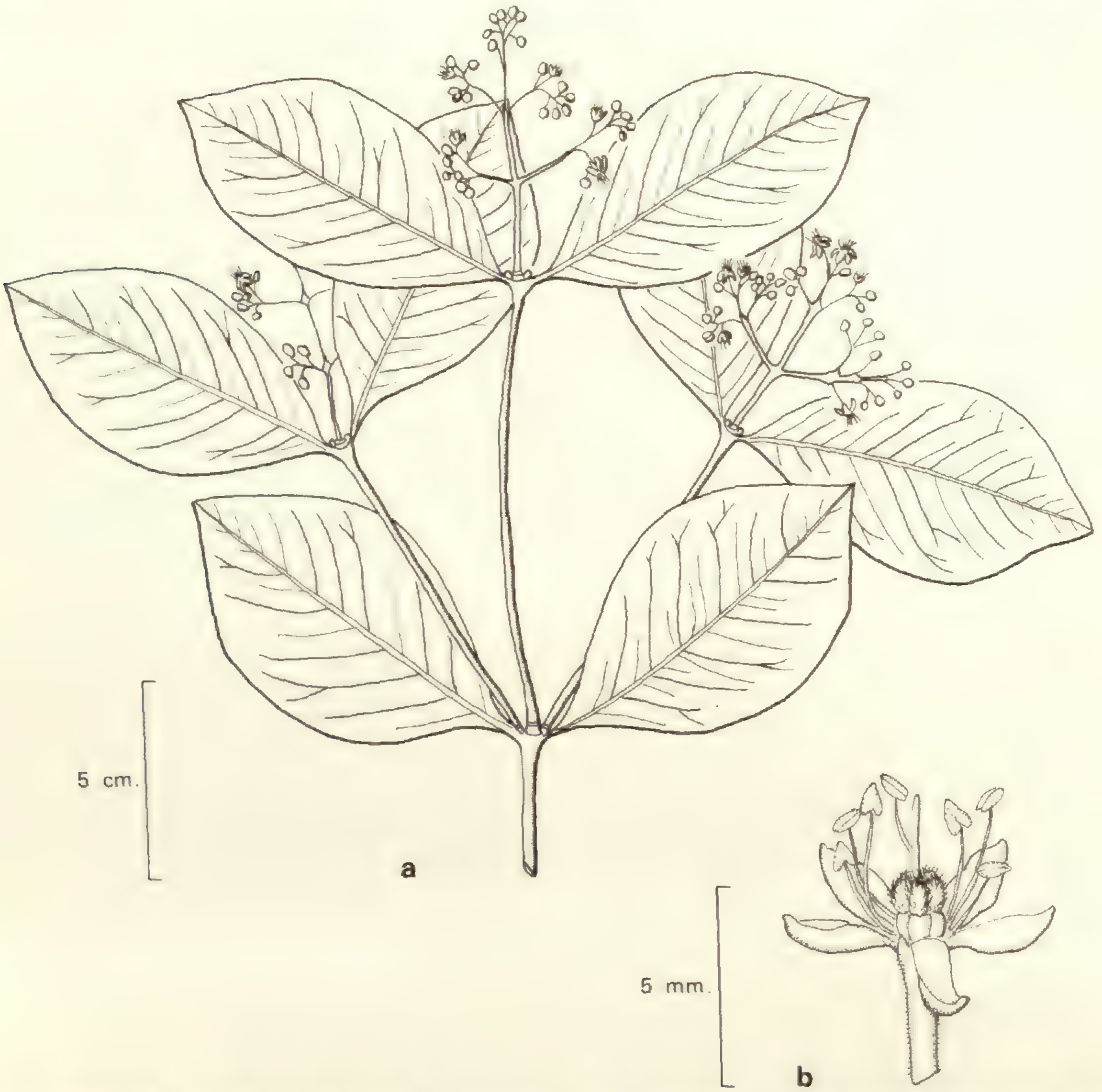


FIGURE 4. *Bosistoa brassii* Hartley var. *brassii*: a, flowering branchlet; b, flower with three stamens removed (both drawn from *Brass 19653*).

A Stephen Johnson collection of *Bosistoa brassii* var. *brassii* (MEL), labeled "upper Gilbert River, 1894," is omitted from the above list because the locality is unlikely. The Gilbert River is on the western side of the Dividing Range, in north Queensland, and flows into the Gulf of Carpentaria.

7b. **Bosistoa brassii** Hartley var. **proserpinensis** Hartley, var. nov.

Arbor parva usque ca. 12 m. alta; ramulis glabris; gemmis glabris; cicatricibus perularum interiorum delapsarum ex cicatricibus perularum exteriorum delapsarum proxime super; foliis unifoliolatis, 5–9 cm. longis; petiolo 1–2.5 mm. longo; foliolo subcoriaceo vel coriaceo, glabro, ovato vel elliptico, 4.5–8.5 cm. longo, 2.5–5 cm. lato, basi obtuso vel rotundato vel subcordato, aequilatero, margine integro, apice obtuso vel acuto, venis primariis utrinsecus costa 11–12; inflorescentia terminali, 7–9 cm. longa,

glabra; floribus ca. 4 mm. longis; sepalis margine ciliatis, aliter glabris, basaliter connatis, anguste triangularibus, 0.5–1 mm. longis; petalis abaxialiter apicem versus puberulis, adaxialiter glabris, ellipticis, ca. 3 mm. longis; staminibus filamentis sublinearibus, antheris ca. 0.8 mm. longis; disco glabro, pulvinato, 0.3–0.4 mm. alto; ovario glabro, ca. 0.8 mm. alto, ovulis in quoque loculo 4–6; stylo glabro, 1.5 mm. longo; folliculis non visis. HOLOTYPUS: *Jones 3857* (CANB).

DISTRIBUTION. East central Queensland, North Kennedy District; foothill rain forests. See MAP 3.

Queensland. NORTH KENNEDY DISTRICT: Mt. Dryander, *Jones 3856* (BRI), *3857* (CANB, holotype), *Moriarty 969* (BRI, CANB); State Forest Reserve 299, Conway Logging Area, *Hyland RFK 4066* (CANB).

The localities cited for this variety are both in the general vicinity of the town of Proserpine; hence the choice of the epithet *proserpinensis*.

Bosistoa brassii is a close relative of both *B. monostylis* and *B. medicinalis*. The pubescence of the ovary in var. *brassii* is similar to that of *B. monostylis*, and the leaves of var. *proserpinensis* are similar in size, shape, and length of petiole to those of some of the unifoliolate specimens of *B. medicinalis*.

EXCLUDED SPECIES

Bosistoa euodiiformis F. Mueller, Frag. Phytogr. Austral. **9**: 174. 1875 = **Acradenia euodiiformis** (F. Mueller) Hartley, Jour. Arnold Arb. **58**: 176. 1977.

Luerssenidendron monostylis Domin, Bibliot. Bot. **22**(89): 289. *t. 29*. 1927 = **Acradenia euodiiformis** (F. Mueller) Hartley, *ibid*. As I pointed out in my revision of *Acradenia*, Domin informally, and incorrectly, referred this species, the sole species of the genus *Luerssenidendron*, to *Pagetia monostylis* F. Mueller. He was followed in this by Engler (in Engler & Prantl, Nat. Pflanzenfam. ed. 2. **19a**: 214, 359. 1931). More recently, Burbidge (Dict. Austral. Pl. Genera 219. 1963) incorrectly placed *Luerssenidendron* in synonomy under *Pagetia*.

ACKNOWLEDGMENTS

I wish to thank the directors and curators of the herbaria listed in the introduction for making specimens in their care available to me. Thanks are also extended to A. G. Floyd, of the New South Wales Forestry Commission Station at Coffs Harbour, and B. P. M. Hyland, of the C.S.I.R.O. Division of Forest Research, Queensland Regional Station, Atherton, for their special efforts in collecting material for me.

INDEX TO EXSICCATAE

The numbers in parentheses refer to the corresponding species and varieties in the text.

Blake *17387* (1a).
Brass *19653* (7a).
Dallachy *287*, *297* (1b).
Dansie *1935* (*QF 62/41*) (7a).
Dietrich *643*, *1436*, *1544*, *1768*, *2212* (6).
Fraser *134* (3).
Hayes, Turner, & McGillivray *2554* (1a).
Henderson *156* (1a).
Herb. Hance *10552* (1b).
Hyland *RFK 1129*, *RFK 2555*, *RFK 2708* (7a); *RFK 4066* (7b); *RFK 4071*, *RFK 4072* (1c); *6180*, *6435* (7a).
Irvine *758* (7a).
Jones *3216* (1c); *3288* (2); *3856*, *3857* (7b).
Macpherson *122* (*North Qld. Herb. 4409*) (1c).
Michael *435* (7a); *708* (1c).
Moore *212* (2).
Moriarty *968* (1c); *969* (7b); *1641* (2); *1642*, *1643*, *1644* (3).
Nugent *11* (1c).
O'Shanesy *86 ser. 9* (1b); *247* (6).
Petrie *8a.* (3).
Scortechini *168* (1a); *305* (1b).
Smith *5137* (3); *10593*, *11831* (7a).
Smith & Webb *3121* (2); *3134* (3).
Stocker *976* (7a).
Thorogood *7* (6).
Webb & Tracey *7047*, *7048*, *8194* (7a); *10067* (1c).
White *1912* (1a); *1940* (3); *10370* (1a).

HERBARIUM AUSTRALIENSE
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ADDITIONAL NOTES ON DIMORPHANTHERA (ERICACEAE)

P. F. Stevens

Recent collections of *Dimorphanthera* F. Mueller, an interesting East Malesian genus in the Vaccinieae with close affinities to the Neotropical genus *Satyria* Klotzsch (Stevens, 1974), and the examination of type material at Bogor, Leiden, and Washington, have necessitated a number of changes in synonymy and the description of three species. These, as well as notes on a few additional species, are given below. A key to all the taxa now recognized in the genus, based on that of Sleumer (1967), may be obtained from the author.

In the following notes, the numbers are those given to the species by Sleumer (1967) in his thorough revision of the genus; those numbers preceded by a "V" refer to species included in *Vaccinium* by Sleumer, but since transferred to *Dimorphanthera* (Stevens, 1974). Herbarium abbreviations are those given in Holmgren, P. K., and W. Keuken, *Index Herbariorum*. ed. 6. Reg. Veg. 92. Utrecht, 1974.

V2A. Dimorphanthera albida P. F. Stevens, sp. nov.

A speciebus aliis Dimorphantherae sect. Pachyanthae in lamina mediocra utrinque glanduloso-punctata, inflorescentia albida racemosa in siccitate brunnea, calyce limbo suberecto 1.8–2.4 mm. longo dentibus circa 1 mm. longis, differt.

Frutex erectus circa 2 m. altus. Ramulus glaber circa 2.5 mm. latus, lineis elevatis rotundatis e petiolis decurrentibus; perulae gemmarum late ovatae circa 1.2 mm. longae et 2 mm. latae. Petiolus 0.6–1.3 cm. longus, glaber; lamina elliptica, (2–)2.5–7.3 cm. longa et (1.2–)1.5–3.5 cm. lata, apice rotundata, basi attenuata, margine subintegra pilis nigris setuloso-glandulis praedita (pari imo basi grandiore quam aliis), utrinque punctis nigris praedita, sed infra punctis densioribus quam supra, pli-nervata, nervis paribus 2 vel 3 usque ad 2 cm. e basi ortis, supra subplana infra valde elevatis, rete venarum utrinque subelevata. Inflorescentiae e axillis foliatis ortae, racemosae, cum 15–20 floribus, axibus 2.5–3 cm. longis, albidis, glabris, valde angulatis; bracteae late ovatae, 3–4.5 mm. longae, glabrae; pedicelli 11–13 mm. longi, angulati, cum calycibus articulati, glabri, bracteolis oppositis late ovatis 3–3.5 mm. longis, 3–4.5 mm. e basibus insertis, haud connatis. Calyx albidus, glaber, tubo 3.5–4 mm. longo et 3.7–4 mm. lato basi rotundata vel subtruncato, interdum versus apicem leviter expansus, limbo suberecto 1.8–2.4 mm. longo, lobis 5 triangularibus circa 1 mm. longis fisso; corolla albida, percrassa, campanulata, 5–7 mm. longa et 6–10 mm. lata (ubi complanata), glabra, fere usque ad basem bistratosa, in lobis 5 triangularibus 2–2.5 mm. longis fissa; stamina 10, ecalcarata, filamentis circa 1.5 mm. longis, versus apicem pilis unicellularibus marginibus et pagina interiore in lineis praeditis, antheris haud lignosis

connectivis pilis praeditis, basibus rotundatis, papillatis, deorsum intendentibus, antheris maioribus circa 3.5 mm. longis, thecis circa 1.5 mm. longis, tubulis divergentibus circa 2 mm. longis poris circa 1 mm. longis, antheris minoribus circa 3.2 mm. longis, thecis circa 1.5 mm. longis. tubulis erectis circa 1.7 mm. longis poris circa 1 mm. longis; ovarium inferum 5-loculare; discus glaber; stylus circa 7.5 mm. longus; stigma circa 0.7 mm. latum, 5-lobatum. Fructus haud cognitus.

TYPE: Papua New Guinea, Morobe District, Bulldog Road, Edie Creek, 2700 m., 5 Aug. 1975, *Vander Kloet 35875* (holotype, A).

DISTRIBUTION. Papua New Guinea, known only from a single collection.

ECOLOGY. *Dimorphanthera albida* was collected in fern heath at 2700 meters altitude; it was in flower in August, the whole inflorescence, apart from the purple anthers and green styles, being white.

Dimorphanthera albida is probably most closely related to *D. ingens* (Sleumer) P. F. Stevens from which it differs in several characters. Its leaf blades are half the size of those of *D. ingens* and have fewer main lateral veins, even in those leaves which are of comparable size and on plants of like size. The inflorescence of *D. ingens* dries blackish rather than brownish, the larger calyx limb is subspreading and has much longer lobes, and the corolla is greenish to pink, never white. Both species have leaf blades of similar shape which are punctate on both surfaces, and many-flowered, racemose inflorescences.

The phellogen of *Dimorphanthera albida* is initiated inside the ring of pericyclic fibers.

It may be noted here that the paratype of *Vaccinium amplifolium* F. Mueller var. *giganteum* Sleumer (equals *D. amplifolia* (F. Mueller) P. F. Stevens), *NGF 8350* (A), is a specimen of *D. ingens*. Its leaf blades are punctate on both surfaces, it has racemose, black-drying inflorescences (they tend to be corymbose in *D. amplifolia*), its pedicels lack glandular hairs, and its flowers, although still in bud, clearly have large calyx lobes.

V3. Dimorphanthera fissiflora (Sleumer) P. F. Stevens.

Honeyeaters and lorikeets are recorded as feeding on the blossoms (*Bulmer 142* (LAE), N. Kaironk Valley, Madang).

7. Dimorphanthera kempteriana Schlechter.

The flowers of this species are used by the local people as a natural lure to catch birds. "Flowers contain nectar which attracts small birds. A noose is placed round the flower and pulled tight as the bird sucks the nectar" (field notes of *ANU 2018* (LAE), Western Highlands).

11. Dimorphanthera amblyornidis (Becc.) F. Mueller.

Dimorphanthera amblyornidis (Becc.) F. Mueller var. **amblyornidis** — see Sleumer, 1967, for references, excl. *D. arfakensis* J. J. Sm.

D. amblyornidis (Becc.) F. Mueller var. *moorhousiana* (F. Mueller) Sleumer — see Sleumer, 1967, for references.

Dimorphanthera amblyornidis (Becc.) F. Mueller var. **steinii** (Sleumer) P. F. Stevens, comb. et stat. nov.

D. steinii Sleumer, Bot. Jahrb. **70:** 117. 1939. TYPE: Nederlands-Neu-Guinea, Weyland Gebirge, 2100 m., 10 Oct. 1931, *Stein 412* (holotype, B, destroyed).

Sleumer (1967) distinguished the two varieties of *Dimorphanthera amblyornidis* by the distribution of indumentum: in *D. amblyornidis* var. *moorhousiana* the pedicel, calyx, outside of the corolla, and disc (usually) were quite glabrous, while in var. *amblyornidis* the outside of the corolla was always puberulent, and the pedicels and disc also often had more or less well developed indumentum. Unfortunately, this separation is not tenable. The majority of the specimens of var. *amblyornidis* have glabrous pedicels (but see below); three which have not, *Gjellerup 1006* (the type of *D. arfakensis*), *Kanehira & Hatusima 13619* (cited as *D. arfakensis* by Kanehira & Hatusima, 1942), and *Kostermans 2275* (all cited as *D. amblyornidis* var. *amblyornidis* by Sleumer, 1961), are to be excluded from *D. amblyornidis*. The first two specimens have anthers which are strongly incurved at the base, the major anthers being 6–6.7 mm. long, whereas in *D. amblyornidis* the anthers are downwardly pointed at the base, the major anthers being up to only 5.5 mm. long. These specimens are discussed below under *D. arfakensis*. In the other collections examined, there are all intermediates between specimens with glabrous corollas and discs (var. *moorhousiana*) and puberulent corollas and discs (var. *amblyornidis*), and specimens with corollas that are clearly puberulent when in bud may be glabrous or almost so at anthesis (e.g. *NGF 47000*, Milne Bay Province). Only two specimens seen have hairs on the calyx and the pedicel: *LAE 56314*, from Milne Bay Province, where the hairs are extremely few, and *BW 6878*, from the Vogelkop, which, although with more obvious indumentum, is no more than sparsely pubescent.

In most floral details the original description of *Dimorphanthera steinii* and the specimens I have seen that have been assigned to it agree with *D. amblyornidis*. The only difference is that in *D. steinii* the calyx and pedicels are "subdensely gray pubescent" (Sleumer, 1967). Sleumer noted that the two species were close, and, in view of the agreement of the two in all matters except for indumentum development, *D. steinii* is reduced to varietal rank under *D. amblyornidis*.

11A. Dimorphanthera arfakensis J. J. Sm. Nova Guinea **12**: 152. *t. 41*. 1914; Sleumer, Bot. Jahrb. 70: 118. 1939. TYPE: Neu-Guinea, Arfak Gebirge, Angi Meer, 1900 m., 26 April 1912, *Gjellerup 1066* (isotype, L).

Dimorphanthera arfakensis may be distinguished from *D. amblyornidis* by its leaves, which are strongly punctate on the upper surface, its more or less turbinate calyx tube which is narrowly attenuate for ca. 1.5 mm. at

the base and only obscurely articulated with the pedicel, and its anthers, which are incurved at the base. The major anthers are 6–6.5 mm. long, and the spurs are free from the tubules for about one third of their length. Although *D. amblyornidis* may have a few glandular hairs on the upper surface of the lamina, they are practically invisible in the adult leaf. The calyx tube at anthesis is usually rounded at the base and is clearly articulated with the pedicel, only rarely being narrowly attenuate for ca. 1 mm.

The status of *Dimorphanthera afarkensis* is still unclear. The characteristics noted above readily distinguish it from *D. amblyornidis*, and *Kostermans 2275* (in fruit) has the indumentum characteristic of the type. However, I have not included *Kanehira & Hatusima 13619* (cited as *D. arfakensis* by Kanehira & Hatusima, 1942) in my concept of *D. arfakensis*. This specimen has anthers like those of *D. arfakensis* (the major anthers are about 6.8 mm. long), but the calyx tube is rounded at the base and is clearly articulated with the pedicel; there are only a few glandular hairs on the upper surface of the lamina. (The duplicate of *Kanehira & Hatusima 13619* at the Arnold Arboretum is in late bud and is not very well pressed.) More collections of this complex from the Vogelkop and from the Moluccas, where the poorly known, but related, *D. pulchra* J. J. Sm. occurs, are sorely needed, but the type specimen of *D. arfakensis* is not part of *D. amblyornidis* as circumscribed above, and it is best to maintain it as a distinct species for the time being.

13. **Dimorphanthera apoana** (Merrill) Schltr.

Dimorphanthera apoana (Merrill) Schltr. var. **apoana** — see Sleumer, 1967, under the species for references.

Dimorphanthera apoana (Merrill) Schltr. var. **mindanaensis** (Merrill) P. F. Stevens, comb. et stat. nov.

D. mindanaensis Merrill, Philip. Jour. Sci. **20**: 418. 1922. TYPE: Mindanao, Misamis Province, Mt. Malindang, 1700 m., *FB 4708* coll. *Mearns & Hutchinson* (holotype destroyed).

Although the type specimen of *Dimorphanthera mindanaensis* has been destroyed, I have seen *BS 38537* (US), the paratype. In details of the flower, including anther type, it is identical to *D. apoana*, except that it has an entirely glabrous corolla. In *D. apoana* the corolla is more or less pubescent outside, but even when Merrill described *D. mindanaensis*, he thought that the character by which he distinguished it from *D. apoana*, corolla pubescence, was one of only moderate weight. Although most specimens of *D. apoana* have yellowish hairs over the whole length of the corolla, in *PNH 1395* such hairs are restricted to the apex. The only other difference separating the two taxa is in the punctation of the lower surface of the lamina: *BS 38537* is epunctate below; the flowering specimens of *D. apoana*, including the type, are punctate below. Both taxa have unicellular hairs on the perulae and petioles. Neither corolla indumentum nor punctation of the lamina is a very strong character in *Dimorphanthera*, so

it seems best to reduce *D. mindanaensis* to varietal rank under *D. apoana*.

Apart from the paratype, one other collection can be placed in *Dimorphanthera apoana* var. *mindanaensis*. *BS 38914* (A, US), from Mt. Candoon, Bukidnon subprovince, Mindanao, is in fruit, but the lower surfaces of its leaf blades are epunctate.

54. Dimorphanthera calodon Sleumer.

This species was reported to be fairly common when initially collected on the Murray Pass, Central Province, but it was not recollected for forty years, despite the rather frequent visits of collectors to this general area. However, it has recently been found along the Bulldog Road, Morobe Province, from 2550 to 2800 meters altitude, and is apparently locally common there. The specimens from the Bulldog Road (*Pratt 17* (LAE), *Allison NG 106* (LAE), *144* (LAE), *Vander Kloet 211875* (A)) agree excellently with the type.

64A. Dimorphanthera napuensis P. F. Stevens, sp. nov.

A speciebus aliis Dimorphantherae in lamina margine crenulata infra punctis haud ornata, inflorescentiis cum 5–10 floribus, corolla in vivo tubulari, mediocra, in siccitate valde complanata, campanulata, et antheris ecalcaratis differt.

Frutex nitens. Ramulus circa 2.5 mm. latus, glaber, lineis elevatis rotundatis e petiolis decurrentibus; perulae gemmarum ovatae, 0.8–2 mm. longae. Petiolus 3–11 mm. longus, glaber; lamina ovata, 3.8–14.5 cm. longa et 2–8.2 cm. lata, apice (breviter) acuminata, versus basem rotundata base decurrens, margine crenulata pilis nigris setuloso-glandulosis in incisis crenulationum et pari pilis similibus sed robustioribus junctionem petioli laminaeque praedita, aliter omnino glabra, venatione pli-nervata, nervis paribus tribus usque ad 1.5(–2.5) cm. e basi ortis, costa et nervis lateralibus supra leviter impressis infra elevatis, rete venatum supra obscura infra leviter elevata. Inflorescentiae e axillis foliatis vel defoliatis ortae, breviter racemosae, axibus (0.4–)1–1.8 cm. longis, glabris; bracteae late ovatae, 1.2–2.2 mm. longae; pedicelli 0.6–1.4 cm. longi, cum calycibus articulati, glabri, bracteolis subopppositis 1.5–2 mm. longis, 1.5–4.5 mm. e basibus pedicellorum insertis, versus axem inflorescentiae connatis ab axe liberis. Calyx viridis, glaber, tubo 2–2.8 mm. longo et 3–3.5(–4) mm. lato basi rotundato, limbo patenti (1.8–)2–2.8 mm. longo, lobis 1–1.4 mm. longis, mucronulatis, marginibus (prope apicem exceptis) incrassatis. Corolla rubra, carnosa, in siccitate subcampanulata, 2.2–3.1 cm. longa et apice 1–1.8 cm. lata, glabra, haud bistratosa, lobis 5 late triangularibus 1.7–2 mm. longis; stamina 10, staminibus maioribus 7.3–8 mm. longis, staminibus minoribus 6–7 mm. longis, filamentis 1.5–2.5 mm. longis, glabris, antheris lignosis ecalcaratis (vel calcaribus minutissimis ornatis — *Brass 11485*), glabris (connectivis pilis parvis adscendentibus praeditis et basibus antherarum papilloso-pilosis exceptis), basibus subacutis plus minusve ad interiorem intendentibus, interdum prope basem appendiculis circa 0.15

mm. longis praeditis (*Brass 11084*), tubulis poris circa 2 mm. longis, antheris maioribus 5–6.2 mm. longis, tubulis leviter divergentibus circa 2.6 mm. longis, antheris minoribus 3.8–4.8 mm. longis, tubulis erectis circa 2.2 mm. longis; ovarium inferum 5-loculare; discus glaber; stylus 3.4–4 cm. longus; stigma circa 1 mm. latum. Fructus haud cognitus.

TYPE: Irian Jaya, environs de Wamena (vallée de la Balim), Napua, 2100 m., 13 Avril 1973, *Raynal 17114* (holotype, P; isotype, A).

DISTRIBUTION. Irian Jaya.

ADDITIONAL SPECIMENS SEEN. **Papuasia.** IRIAN JAYA. Snow Mountains: Wiligimaan, Baliem, 2000 m., *BW 12555* (A); Bele River, 18 km. N.E. of Lake Habbema, 2350 m., *Brass 11485* (A); Bele River, 2200 m. camp, *Brass 11084* (A).

ECOLOGY. *Dimorphanthera napuensis* is a sprawling or scandent shrub growing in valley forest, forest openings, or young secondary forest from 2000 to 2350 meters altitude. Specimens in flower have been collected in April, June, and November.

LOCAL NAME. "Howaijok" (Dani).

Dimorphanthera napuensis may be recognized by its strongly crenulate leaf margins, its entirely glabrous leaves (apart from the marginal, black, setular-glandular hairs), its shortly racemose inflorescences with 5–10 flowers, its easily flattened, tubular corolla (which becomes subcampanulate on drying), and its ecalcarate (or practically so) anthers. It has been confused with *D. wrightiana* (Koord.) J. J. Sm. (incl. *D. d'armandvillei* J. J. Sm.), but that species has leaf blades which are cuneate to rounded at the base and entire at the margin (although there are setular-glandular hairs there). *Dimorphanthera wrightiana* also usually has ca. three-flowered inflorescences (up to seven-flowered in the type of *D. d'armandvillei*?) and the flowers themselves are relatively thickly carnose, drying tubular and less than 2 cm. long.

Flowers of *Dimorphanthera napuensis* preserved in alcohol have an erect calyx limb and a cylindrical corolla 3.1 cm. long and 1.4 cm. across that is gradually narrowed both towards the base and the apex, the latter being 1.1 cm. across.

The phellogen in the stems of *Brass 11084* is initiated inside the ring of pericyclic fibers. All specimens have a two-layered hypodermis, although it is locally three-layered in places in *Brass 11084*.

64B. Dimorphanthera wisselensis P. F. Stevens, sp. nov.

A speciebus aliis Dimorphantherae in folia subovata margine integra pilis setuloso-glandulosis destitutae sed pagina infra arcte nigro-punctata, inflorescentia pauciflora subfasciculata, pedicellis tenuibus, flore tubuloso probabiliter tenuiter carnoso in siccitate subcampanulata, et antheris ecalcaratis differt.

?Liana. Ramulus circa 2 mm. latus, glaber, lineis elevatis rotundatis e petiolis decurrentibus; perulae gemmarum ovatae, circa 2 mm. longae. Petiolus 6–10 mm. longus, glaber; lamina plus minusve ovata, 7.1–10 cm. longa et 2.3–3.6 cm. lata, apice acuta, base acuta vel cuneata, margine integra, pilis setuloso-glandulis etiam basi, ut videtur, destituta, pagina infra subdense glanduloso-punctata, venatione pli-nervata, nervis lateralibus paribus 2–3 usque ad 1.5 cm. e basi ortis, costa et nervis lateralibus supra subimpressis infra elevatis, rete venarum supra obscura infra leviter elevata. Inflorescentiae subfasciculatae e axillis defoliatis ortae cum circa 6 floribus, axibus usque ad 3 mm. longis; bracteae ovatae, circa 1.5 mm. longae; pedicelli 2.2–3 cm. longi et circa 0.5 mm. lati, cum calycibus articulati, glabri, bracteolis subopppositis circa 1.5 mm. longis, 3–5 mm. e basibus pedicellorum insertis, versus axem inflorescentiae subconnatis ab axe liberis. Calyx glaber, tubo 2–2.5 mm. longo et 2.3–3.2 mm. lato basi rotundato vel truncato, limbo subrecurvato circa 0.8 mm. longo, fere usque ad basem in lobis 5 triangularibus diviso; corolla tenuiter carnosa, in siccitate subcampanulata, 1.6–1.9 cm. longa et 0.8–1.2 cm. lata, glabra, haud bistratosa, lobis 5 triangularibus circa 3 mm. longis; stamina 10, staminibus maioribus circa 6.8 mm. longis et staminibus minoribus circa 5.2 mm. longis, filis circa 1.5 mm. longis, versus apices marginibus pilis praeditis, antheris lignosis, basibus leviter incurvatis, glabris (pilis connectivis praeditis exceptis), antherae maioribus circa 5 mm. longis, tubulis leviter divergentibus circa 3 mm. longis, poris circa 2 mm. longis, antheris minoribus circa 3.7 mm. longis, tubulis erectis circa 2 mm. longis, poris circa 1.2 mm. longis; ovarium inferum 5-loculare; discus glaber; stylus circa 2.3 cm. longus; stigma vix expansum. Fructus haud cognitus.

TYPE: Dutch New Guinea, Wissel Lake Region, Bivouac XII–Bivouac XIV, 7 Jan. 1939, *Eyma 4247* (holotype, BO).

DISTRIBUTION. Known only from the one collection from Irian Jaya.

Dimorphanthera wisselensis may be recognized by the total absence of setular-glandular hairs on the margin of the lamina, apparently even at the base, and the presence of glandular spots on the lower surface of the lamina, the small inflorescence, the relatively long, slender pedicels, the short calyx lobes, the small corolla that flattens on drying, and the ecalcarate anthers.

Eyma 4247, the type specimen of *D. wisselensis*, was cited as *D. wrightiana* by Sleumer (1961), but the characters noted above readily distinguish it from that species.

66. Dimorphanthera tedentii P. F. Stevens.

The ovaries of this species were described as being 5-locular; they are, in fact, incompletely 10-locular. (*Dimorphanthera amoena* Sleumer and *D. velutina* Schltr. are the only other species with similar ovaries.)

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NOTES FOR THE FLORA OF DOMINICA: SPERMACOCE CONFUSA AND SCHRADERA EXOTICA (RUBIACEAE)

DAN H. NICOLSON

THIS PUBLICATION constitutes another contribution largely arising from the Bredin-Archbold-Smithsonian Biological Survey of Dominica (1964–1970) which sent about twenty actively collecting botanists to Dominica for up to three months each. Their collections, as well as those of earlier and subsequent botanists, provide the basis for preparing the dicots for the *Flora of Dominica* initiated by W. H. Hodge (1954), who completed the ferns, fern allies, gymnosperms, and monocots. With the help of Richard A. Howard, who volunteered a preliminary checklist of the dicots of Dominica, and a number of specialists who have contributed various families, we are very close to completion, only eight of 118 dicot families still to be done. This particular publication is intended to take care of more extensive nomenclatural comments than are usual in floristic works.

The comment by my respected colleague, F. Raymond Fosberg, that my method of citing references in synonymies is "unfortunate" impels me to explain why it was adopted. The references in synonymies appear in "short form" but are fully expanded in the bibliography, including titles, pages (or volumes), and dates of each complete article or work. It has struck me as mildly anomalous that botanists should handle references in synonymies (in "long form," with author, abbreviated title, page, and date; nothing in the bibliography) differently than they handle the same reference in texts (in "short form," with author, date, and page; full expansion in the bibliography).

Experienced botanists are used to the abbreviated titles and normally have no difficulty recognizing the correct title without the help of expansion in the bibliography. Others will perceive the abbreviated titles of "long form" for what they are, jargon, known only to the cognoscenti. Of course, the jargon is part of taxonomic literature (cf. Index Kewensis), and its mastery will continue to be part of a botanist's apprenticeship. The taxonomist who cannot remember that "Sw. Prod." is Swartz's *Nova Genera & Species Plantarum*. . . . will forever be at a disadvantage in dealing with West Indian botany. However, that does not mean that we cannot try to avoid the jargon.

It seemed appropriate to attempt consistently to use "short form" in a floristic work, the *Flora of Dominica*. I am not yet advocating it,[1] merely trying it. It is used in this short paper because it is easier to maintain the format of the *Flora of Dominica*.

The main problem of "short form," beyond the necessity of checking the original publications for full titles and pagination for the bibliography,

[1] The editorial board of this Journal does not advocate this method either, but is willing to accept an example of Dr. Nicolson's experiment. — *Eds.*

is dealing with different publications in the same year by the same author. In a bibliographically rich work, such as a flora, one never knows whether or not this will occur until one is finished. In order to avoid retroactive and constant revisions of completed work, I have opted to add an abbreviated title reference in support of the date whenever a particular publication spans more than a year. Although this looks like and can function like the abbreviated titles of "long form," it is really only a possibly necessary clarification of the usual "short form" reference to the fully expanded reference in the bibliography.

Spermacoce confusa Rendle, 1936 (Jan.), p. 12; Fawcett & Rendle, 1936 (July), Fl. Jam. 7: 120; Gillis, 1974, p. 185.

Spermacoce tenuior sensu auct. plur., non Linnaeus, 1753, p. 102; Gaertner, 1788, Fruct. 1: 122. *t. 25, f. 9*; Bacigalupo, 1972, p. 344, *f. 1.* (For more citations, see Fawcett & Rendle, 1936, Fl. Jam. 7: 120, and Gillis, 1974, p. 185.)

Leaves paired, rough above; inflorescences few-flowered; stamens included; calyx lobes equal; capsule crustaceous, hirtellous; the cocci attached, unequal, one with three calyx lobes and closed, the other with one calyx lobe and open; seed glossy brown, finely reticulate.

Neotropics; in Dominica as a roadside weed: Pointe Ronde (*Hodge 2639*).

Note: The possibility that the Linnaean binomial, *Spermacoce tenuior*, was being misapplied was first argued by Rendle (1934) when he demonstrated that *S. tenuior*, described by Linnaeus (1753, p. 102) as "*glabra*," had come to be misapplied to a scabrid species. He traced the typification to specimens of Dillenius cultivated at the Hortus Elthamensis and clarified the reasons for the subsequent misapplication. He concluded that what was then called *S. riparia* Chamisso & Schlechtendahl was actually *S. tenuior* Linnaeus, and what was then called *S. tenuior* probably should be called *S. remota*.

In a subsequent paper, Rendle (1936) reported study of the type material of *S. remota* Lamarck, showed that it is a distinct species, and proposed a new species (erroneously calling it a *nomen novum*, correct only for renaming a taxon with a validly published but illegitimate name, not for naming a new species with a misapplied name), *S. confusa* Rendle, for *S. tenuior* sensu auct. Gillis (1974), feeling that the name was not validly published because it lacked a Latin description, provided one. However, I believe that Rendle satisfied the requirements in Article 36 for valid publication by "reference to a previously and effectively published Latin description or diagnosis of the taxon" when he cited "K. Schumann in Martius, Flor. Brasil. (vi. 6, p. 33)." I regard the citation of p. 33 as a correctable slip of the pen for p. 34, on which Schumann's Latin description of *S. tenuior* sensu auct., non Linnaeus, appears. I grant that the reference appears in the early part of the paper in an explanation of why

he earlier thought *S. remota* Lamarck to be an applicable name, two pages before he actually proposes *S. confusa*. However, despite the separation of the validating reference to a Latin description of the taxon from the new species itself, it seems to me that Rendle has, in fact, satisfied the spirit and letter of Article 36.

Bacigalupo (1972) rejected Rendle's lectotypification, adopting another Dillenian specimen found by Burkart which had been overlooked by Rendle. However, I cannot accept her lectotypification for the Linnaean name since it is contrary to Linnaeus's own description of *S. tenuior* as "*glabra.*" What she calls *S. tenuior* I would call *S. confusa* Rendle, and what she calls *S. riparia* I would call *S. tenuior* Linnaeus. It is clear that Dillenius mixed elements of *S. confusa* (with scabrid leaves and hirtellous capsule) and *S. tenuior* (with glabrous leaves and capsule). Irrespective of how one might lectotypify the Dillenian pre-1753 taxon (*Spermacoce verticillis tenuioribus* Dillenius), it seems apparent that the Linnaean name must be typified on a glabrous element.

Schradera exotica (J. F. Gmelin) Standley, 1929, p. 286.

Urceolaria exotica J. F. Gmelin, 1791, Syst. Nat., ed. 13, **2:** 390; Standley in N. Am. Fl., 1921, **32:** 132.
Schradera capitata sensu Vahl, 1796, Eclog. **1:** 35. *t. 5* (as to Monserrat material, not as to synonym, *Fuchsia involucrata* Swartz).
Schradera capitata Vahl ex Willdenow, 1799, Sp. Pl. **2:** 238, later homonym.
Urceolaria capitata Fritsch, 1894, p. 288, *nom. superfl.*
Schradera vahlii Steyermark, 1964, p. 277, *nom. superfl.*
Schradera vahlii var. *acutifolia* Steyermark, 1964, p. 277.

Succulent liana or shrubby tree to 7 m.; stipules membranous, more than 1 cm. long, deciduous, lower half united; inflorescence terminal, a pedunculate head subtended by a peltate involucral bract; flowers white; berry white and fleshy.

Hispaniola to Grenada; infrequent to common in Dominica on slopes from 400 to 850 m.: Morne aux Diables (*Nicolson 1935*), En Haut Jean (*Webster 13513*), Pont Cassé area from Deux Branches to Castle Bruce turnoff (*Ernst 1671, Stern & Wasshausen 2546, Wilbur 7749*), Freshwater Lake area (*A. C. Smith 10289, Gillis 8220, Wilbur 7394*), Breakfast River (*Hodge 1892*), lower slopes of Morne Plat Pays (*Wilbur 7855*).

Note: The nomenclature of this species has been controversial. The synonymy above indicates that this species has been called *Urceolaria exotica* (1791, 1921), *Schradera capitata* (1796, 1799), *Urceolaria capitata* (1894), *Schradera exotica* (1929), and *Schradera vahlii* (1964). There are several points of disagreement of which the first, *Urceolaria* vs. *Schradera*, has been settled by conservation of *Schradera* and rejection of *Urceolaria*. A second point, raised by Fritsch (1894), questions the validity of publication of *Urceolaria exotica* Gmelin (1791). This really is a question of whether or not a reference (by Gmelin) to an earlier generic

description (by Willdenow) can validate a specific name. Fritsch (1894) argued that the species was not separately diagnosed and could not be accepted. The I.N.G. staff reviewed this question, and I agree with their position that, under Article 32, there is no requirement that a species be validated by a reference to a description of the taxon *in the same rank*. It is true that Article 41 specifically precludes validation of generic names by reference to an earlier description, unless the description is of a "genus in that rank or as a subdivision of a genus," thus specifying rank. However, there is no comparable language specifying rank for a description validating a species name, as long as the later author means the same taxon as the earlier; that is, that the generic taxon is monotypic. Gmelin (1791) provided many specific epithets for monotypic genera published by earlier authors of "Genera Plantarum," such as Jussieu and Schreber. These are accepted and to be seen in Appendix III of the Code: *Cansjera rheedii*, the type species of *Cansjera*, *Securinega durissima*, the type species of *Securinega*, not to mention *Urceolaria exotica*, the type species of *Urceolaria*.

Steyermark (1964) argued that *Urceolaria exotica* Gmelin is rejectable as a *nomen confusum* under Article 69, because Standley (1921) applied the name to a concept including *Schradera capitata* of the Antilles, *S. brasiliensis* of Brazil, and *S. cephalophora* of Cuba, all regarded by Steyermark as distinct species. I reject the argument that *Urceolaria* (*Schradera*) *exotica* has been used in different senses and has become a source of error. The binomial has always included the Antillean element and, although applied to a broader species concept, has never been restricted to a species concept excluding the type, as specified in the examples given for Article 69. In any case, the Leningrad Congress modified this Article to establish a list of *nomina specifica rejicienda*, and it can now be invoked only by having a name proposed and accepted for rejection.

Another problem arose when Vahl (1796) published *Schradera capitata* and included an earlier name, *Fuchsia involucrata* Swartz (1788), in synonymy. This constitutes a superfluous name under Article 63 for which Article 7, paragraph 10, requires automatic typification of *S. capitata* Vahl, *nom. illeg.*, on the type of the Jamaican type of *Fuchsia involucrata* Swartz. Willdenow (1799), realizing Vahl's error, excluded the offending synonym, thereby creating a new *Schradera capitata*, a later homonym, with a different type than that of Vahl's earlier binomial.

Fritsch (1894) created *Urceolaria capitata* Fritsch, probably based on *Schradera capitata* Willdenow (later homonym) but possibly based on *Schradera capitata* Vahl (superfluous name). In any case, Fritsch's name is based on an illegitimate basionym and, under Article 72, Note, is to be treated as a new name, not a new combination. However, Fritsch erroneously rejected the earliest available name, *Urceolaria exotica* Gmelin, and his new name must be regarded as a superfluous renaming of *Urceolaria exotica*.

Another problem arose when Standley (1929) published *Schradera exotica* (J. F. Gmelin), comb. nov., based on *Urceolaria exotica* J. F.

Gmelin. He added another synonym, *Schradera capitata* Vahl, without excluding its earlier synonym and obligate type, *Fuchsia involucrata* Swartz, suggesting that his binomial might be another superfluous renaming of *Fuchsia involucrata* Swartz. However, the last paragraph of Article 55 is very clear that a new combination must be typified on the type of its basionym, irrespective of the circumscription of the taxon to which it was applied or, more particularly, misapplied. The last paragraph of Article 63 is also pertinent.

Thus, under the present Code, I can see no barrier to acceptance of *Schradera exotica* (J. F. Gmelin) Standley and reject *Schradera vahlii* Steyermark as a superfluous name.

Taxonomic note: Steyermark (1964, p. 277) recognized *Schradera vahlii* var. *acutifolia* Steyermark from two Dominican collections (*A. C. Smith 10289*, holotype, from Freshwater Lake, and *Lloyd 185*, paratype, from Laudat). He regarded the presence of an acute to subacuminate leaf apex combined with an acute to subacute leaf base as a rare variation in a species in which the apex is normally obtuse and the base varies from rounded or obtuse to subacute. Study of topotypes (*Gillis 8220* and *Wilbur 7394*) shows the typical obtuse to subacute leaf apices and subtruncate to obtuse leaf bases, suggesting this taxon could hardly be more than a forma. In addition, study of the isotype indicates that it is in young bud or flower and that the leaves may be unexpanded. Study of seven other Dominican collections indicates that the narrowest and most acute leaves are typical of the youngest and outermost leaves. *Webster 13513* is particularly instructive, the leaves ranging from being small and acute (5 × 2 cm.) to large and broad (11 × 7 cm.). Survey of 25 specimens from other islands indicates variability in leaf shape from rather narrow to quite broad. Curiously, the narrowest and broadest leaf shapes are on Dominica. In conclusion, I cannot accept the existence of a distinct narrow-leaved taxon on Dominica, even as a variety.

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